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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

160th Session (1947–48)

Vol. 160 Part 2

CONTENTS

Page

Proceedings, 22 April 1948 to 24 May 1948, including papers printed in abstract 73

Papers printed in full,—

THE HOOKER LECTURE. The Mechanism of Evolution. By D. M. S. Watson 75

A Discussion on the Orientation of Birds on Migratory and Homing Flights

Recent biological evidence for the methods of bird orientation. By W. H. Thorpe 85

Some physical principles of bird orientation. By D. H. Wilkinson 94

Polish investigations on homing in birds and their orientation in space. By R. J. Wojtusiak 99

General Discussion 108

Tropical Fungi.—III. New species and revisions. By C. G. Hansford 116

Non-sexual reproduction in sponges, with special reference to a collection of young *Geodia*. By M. Burton 163

Edmund Davall, F.L.S., an unwritten English chapter in the history of Swiss Botany.—Final Addendum. By G. R. de Beer 179

Obituaries 185

Additions and Donations to the Library 193

Benefactions 196

Index, Title-page and Contents

Editorial Note.—To facilitate citation, it has been decided to give the 'Proceedings' Volume-numbers, beginning with Vol. 158, which has been chosen as the arbitrary number and which agrees with the number of the Session.

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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

Session 1947–48

Vol. 160 Part 2

PROCEEDINGS OF THE GENERAL MEETING ON 22 April 1948

Professor G. R. DE BEER, F.R.S., President, in the Chair.

The Proceedings of the General Meetings, held on Thursday, 11 March and Tuesday, 16 March 1948, having been circulated, were taken as read and confirmed.

The President reported that the Treasurer and himself had attended at Buckingham Palace when H.R.H. THE PRINCESS ELIZABETH, L.G., F.R.S., signed the Roll and Charter Book of the Society. The vellum sheet as signed was displayed.

The following were thanked for gifts made to the Library since the last meeting :—Mr. K. C. Corsar, Dr. Alfred Ernst, Dr. Marthe Ernst-Schwarzenbach, Mr. O. B. Miller, Dr. B. Sahni, Prof. James Small, Capt. F. Kingdon Ward and Messrs. Methuen and Co., Ltd.

Dr. W. B. TURRILL was by show of hands elected an Auditor in place of Mr. A. H. G. Alston, who was unable to serve.

Certificates of recommendation for election to Fellowship of the candidates named in the Agenda of the General Meeting to be held on 22 April 1948 were taken as read for the second time.

Certificates of recommendation for election to Fellowship, in favour of Edward Augustine Ellis, Stanley Arthur Manning, Professor Alastair Worden and Professor Vero C. Wynne-Edwards were read for the first time.

Read for the second time certificates of recommendation for election to Foreign Membership, in favour of Professor Louis Fage, Académie des Sciences, Paris, and Professor August Weberbauer, Universidad de San Marcos, Lima, Peru.

The President reported the deaths of Miss Edith Isabel Grindley, Mr. James Lawrence Chaworth-Musters and Professor Frederick Orpen Bower, F.R.S., Fellows of the Society.

The following communications were read and discussed :—

Mr. H. H. Crane. Viridescence in *Primula denticulata*. (Exhibit.) (Discussed by Dr. B. Barnes.)

Dr. B. Barnes. White flowers in *Ranunculus Flammula* Linn. (Discussed by the President, Dr. W. B. Turrill and Mr. F. C. Grigg ; Dr. Barnes replied.)

Abstract.—

The white-flowered variety of *Ranunculus Flammula* L., which was described to the Society on 27 November 1941, had not reappeared in the original locality up to August, 1947.

Prof. W. E. Le Gros Clark, F.R.S. A review of the African fossil Primates discovered during the year 1947. (Discussed by the President, Dr. A. Tindell Hopwood and Prof. A. J. E. Cave ; Prof. Le Gros Clark replied.)

Abstract.—

During last year, a number of important discoveries of fossil Primates has been made in Africa. In South Africa, Dr. R. Broom, F.R.S., has collected far more complete material of the Australopithecinae than had previously been found. These new discoveries were considered in relation to the earlier material, and, with Dr. Broom's generous permission, lantern-slides of some of the new specimens were shown. In East Africa, the British-Kenya Miocene Expedition, under the leadership of Dr. Leakey, has led to the collection of a remarkable quantity of fossil ape material from Early Miocene deposits in Kenya. These fossils are now being studied in the Department of Anatomy at Oxford, and a preliminary account of them was given.

The Meeting was then adjourned until Thursday, 29 April, 1948.

PROCEEDINGS OF THE ADJOURNED GENERAL MEETING ON 29 April 1948

Professor G. R. de Beer, F.R.S., President,
in the Chair.

The following were thanked for gifts made to the Library since the last meeting :—Mr. Vladimir Asmous, Dr. W. E. Swinton and the Royal Botanic Gardens, Kew.

The following Fellow signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—Mr. Gilbert Young Kennedy.

Certificates of recommendation for election to Fellowships, in favour of Edward Augustine Ellis, Stanley Arthur Manning, Professor Alastair Worden and Professor Vero C. Wynne-Edwards, were read for the second time.

Candidates for membership were balloted for and elected :—

Fellowship.—Captain Harry Walter Abbiss, M.B.E., D.C.M., M.M., G. Abdin, M.Sc., Ph.D., Professor Emmanuel Ciprian Amoroso, M.D., Ph.D., Austin Edward Armitage, Archibald Park Balfour, Sachindranath Banerjee, M.Sc., Miss Kathleen Mary Bayne, B.A., Arthur Paul Benthall, Gerald Anthony Best, Roger Bevan, B.M., B.Ch., M.R.C.S., L.R.C.P., Albert Edward Blake, K.L.B., Ralph Anthony Blakelock, B.Sc., Elsie Burrows, B.Sc., Ph.D., Maurice Burton, D.Sc., Miss Mary Gordon Calder, B.Sc., Ph.D., the Hon. Anthony Freskyn

Charles Hamby Chaplin, Syama Prasad Roychaudhury, M.Sc., Madhab Chandra Das, M.Sc., Charles George Maurice de Worms, M.A., Ph.D., C. L. Duddington, M.A., Felix Durocher Yvon, Miss Honor Bridget Fell, D.Sc., Ph.D., William Arthur Fell, M.D., Alan Fisk, M.Sc., Professor Theodore Thomson Flynn, D.Sc., Edmund Brisco Ford, M.A., D.Sc., F.R.S., Peter Ford, B.Sc., Ph.D., Professor Kenneth James Franklin, M.A., D.M., F.R.C.P., William Stuart Fraser, Frederick Clifford Fryer, Arthur Lionel Goodday, Rev. Arthur George Gregor, M.A., B.D., Philip Herries Gregory, B.Sc., Ph.D., Peter Greig-Smith, B.A., J. P. Harding, M.A., Ph.D., Richard J. Harrison, M.A., M.B., M.R.C.S., L.R.C.P., A.L.S., Stuart Frederick Hayes, B.Sc., Arthur George Lee Hellyer, Bertram Maurice Hobby, M.A., D.Phil., Mrs. Agnes Margaret Hughes, B.Sc., Charles Norman Carlyle Jayawardena, B.A., John William Jones, B.Sc. Ph.D., Abdus Sattar Khan, B.A., M.Sc., Harvey Goodall Langham, John Withers Lester, Miss Patricia Lewis, B.Sc., George Donaldson Lockie, the Hon. David Bowes-Lyon, Professor Brian J. Marples, Henry Samuel Amos Marshall, Major H. I. Matthews, M.C., Professor D. M. Munshi, B.Sc., Jack Raleigh Henchman Nash-Wortham, Ernest Nelmes, David Richmond Newth, B.Sc., Ronald Gordon Newton, B.Sc., Ph.D., Sanya Dojo Onabamiro, B.Sc., Brian Leslie Perkins, Joseph Henry Garfield Peterken, Dr. Rodolfo Emilio Giuseppe Pichi-Sermolli, James Wilmot Ogden Platt, Arthur Alfred Prestwich, John Pryce-Jones, Qadir Hosain Qureshi, M.Sc., Donald Rhind, O.B.E., B.Sc., James Philip Cuming Russell, Major George Sherriff, Professor V. H. Simonian, Ph.C., Mrs. Christine Mary Snow, M.A., B.Sc., Professor Julio Maria Sosa, M.D., Harry Stansfield, M.Sc., Miss Ellen Mary Stephenson, M.Sc., Neville George Stephenson, M.Sc., William Leslie Sumner, B.Sc., Ian M. C. Talman, Henry Gerard Thornton, D.Sc., F.R.S., Helen M. Townley, B.Sc., the Hon. Andrew Nicolas Armstrong Vanneck, M.C., David Allardice Webb, M.A., Ph. D., John Webster, B.Sc., Miss Mabel B. Whitaker, B.Sc., Donald James Butt White, B.Sc., John Edward Miles Williams, B.A., George Stanley Woodcock, Alfred Samuel Wright.

Foreign Membership.—Professor Louis Fage and Professor August Weberbauer.

Associateship.—Peter James Wanstall, B.Sc.

The following communication was read :—

THE HOOKER LECTURE.

Professor D. M. S. Watson, F.R.S., delivered his Lecture on 'The Mechanism of Evolution'. [Printed in full, below.]

The President expressed the thanks of the Meeting to Professor Watson for his Lecture.

THE HOOKER LECTURE

THE MECHANISM OF EVOLUTION.

By D. M. S. Watson.

General acceptance of the view that the existing conditions of life in the world, both of the animal and plant kingdoms, had arisen by slow continuous modification of those of the past, followed from that meeting of the Linnean Society at which Charles Darwin and Alfred Russel Wallace independently set out a mechanism whereby this evolution could have been brought about. In Darwin's words, 'species arose by the preservation of favoured races in the

struggle for life'. Races were favoured because the individuals of which they were composed were specially adapted by their structure, and by the habits associated with that structure, for life under the special circumstances in which they lived.

This idea of the special adaptation of species of animals to specific circumstances is an old one ; it forms part of the argument of Paley's ' Evidences ' and dates back, I believe, to John Ray and the XVIIth-century naturalists. In the early days of the discussion of the Darwinian theory the view received wide assent, but I think that botanists, to a larger extent than zoologists, demurred to the view of a detailed interlocking of structure and environment on the grounds that plants of very diverse kinds lived side by side, obviously exposed to exactly the same external conditions. But Darwin, throughout the period of his work on the ' Origin of Species ', was in close association with Joseph Dalton Hooker, traveller and botanist, not only a great systematist, but a great naturalist and gardener, who was, perhaps, more capable than anyone else of his day of giving to Darwin a balanced view of plant conditions in nature. Subsequent work has on the whole made clear that the restriction of each species to places with a limited range of external conditions is generally true, but that the relationship is, in most cases, scarcely so close as Darwin apparently believed.

This matter of adaptation of species is an important one. A close fit is seen, perhaps in an exaggerated form, in the relationship of a parasite to its host. The existence of a parasite, especially of one which lives in the tissue of a plant stem or of another animal, implies a whole series of chemical compatibilities and when, as in Trematodes, the parasite during a life-cycle may pass through four independent and different animals, the adaptation becomes immensely elaborate. The true Darwinian doctrine would imply that these adaptations have been gradually achieved through a series of approximations, a process which would require immense time and whose intervening stages are most difficult to conceive. But in fact the adaptation, although it exists, and necessarily exists, may well be a purely accidental one. It appears to be true that only one of the very many pond snails of Britain acts as a host for the early stages of the sheep liver-fluke *Fasciola hepatica*, and it should therefore be the case that this parasite cannot maintain itself in any place to which sheep may be taken in the absence of this particular snail ; but in fact Australian sheep, in a country where *Limnaea truncatula* does not occur, are infected by this parasite just as are those in this country. There a *Bulimus* is said to be their intermediate host, and, as *Fasciola* is clearly in origin a sheep parasite, there has never been an opportunity for the building up of a specific adaptation of its early stages to the *Bulimus* which is restricted to Australia, where no sheep lived until they were introduced some hundred and fifty years ago. In fact we have here the exploitation of purely accidental compatibility happening to exist without any process of gradual establishment. It is, I think, an example of pre-adaptation in Cuénot's sense. It seems to me extremely probable that the original adaptation to *Limnaea truncatula* was equally accidental and that a great many similar cases of adaptation are of the same kind—an animal through accident finds itself with certain qualities which do in fact fit it for life under some special circumstances different from those to which its ancestors were accustomed.

It is now, I think, generally believed by biologists that a species is a group consisting of all its living individuals, together with many now dead, and others not yet born, any individual of which is in principle capable of breeding with any other individual of the opposite sex and thus producing fertile offspring, whilst the individuals of the species do not in ordinary circumstances of their natural life interbreed with individuals of any other species, or at any rate, do not produce fertile offspring if they do so. In fact, in a great many cases, the

essential specific quality is this restricted power of breeding. Through investigations, especially of cytologists, we now know that any one of a large number of chromosomal changes, accidental in their occurrence in that they may be induced by radiation, or by the action of such chemical substances as mustard gas, may lead to the production of infertility. Indeed, it now seems likely that the origin of species is, in general, an accidental effect which may occur without the production of any recognisable morphological changes, as in the case, for example, of *Drosophila melanogaster* and *D. simulans*.

There are living perhaps one million species of animals and very many plants, and such an immense diversity of life implies an astonishing number of accidents in the past, fortunate accidents in that each of them has proved viable and has allowed the new form which it produced to have maintained itself for many generations. Of course, those which were non-successful must clearly have been vastly more numerous, and imply that such accidental events are constantly occurring, but why should they not be ? We know from laboratory experience that new mutations of genes arise constantly at a determinable rate. Haldane has shown that a similar mutation rate occurs in ordinary human populations, and we know that recessive mutations are present in large numbers in many wild stocks of insects and other animals. We know from the evidence derived from the decay of radioactive substances that life is represented by fossils extending back for some five hundred million years, and that the world existed in such a form that stratified rocks could be laid down under water for one thousand five hundred million years before the first actual appearance of the remains of animals in the geological succession. Man is the most abundant mammal—a thousand million individuals are now living—but the number of living individuals of a common copepod must be enormously greater, and each one during its life produces a considerable, in some cases a very large, number of gametes. In fact, over the whole period of existence of living beings the total number of gametes which have been produced is fantastically great, giving full scope for the appearance of these changes of a structural kind which have been the basis of all evolution. But even if we believe that species and their apparent adaptations to a special ecological circumstance be accidental, and that the adaptations may thus have been to a very large extent pre-adaptations, there still remain many cases in which adaptation in its natural meaning has in fact occurred.

Nevertheless, there are instances in which it is very difficult to believe that adaptation has played any important part in evolution. If you examine a series of the remains of animals collected from a geological formation which, like the English chalk, represents one ecological type, uniform or very nearly so over a considerable period of time, you find that in very many cases it is possible to distinguish a group of specimens from a high horizon from a similar group from a low one, even though it be impossible to find evidence to show that the two groups belong to different species. In these circumstances it is sometimes possible to show that the change in character from the bottom to the top is continuous, even though it be statistical in nature, a change in the proportion in which certain structures are represented in the population, rather than a sudden break with the introduction of a new form. But if, instead of dealing with the minor structural characters of an echinoderm test, or a mollusc shell, we consider the changes which take place in the skeleton of a mammal, we may find that these changes proceed in a way which remains essentially constant throughout a period which may represent perhaps some twenty million generations, and that the effect is to bring about changes which increase the efficiency of the animals which display them, often not in relation to some very restricted habitat, but for life under a variety of conditions. Such changes, even although they proceed by alterations in the proportion in which definite qualities be present in a population, are true adaptations ; they are adaptations to life in general and not with

regard to some particular set of environmental conditions. The classical cases are found amongst mammals, where we now have very extensive material from all over the world, and where we know a great deal about the physiology and the requirements of several living forms. It is this type of evolution, a change proceeding slowly, and commonly in a similar manner in large divisions of the animal kingdom—in families or even in orders which has really been responsible for the structural diversity of the animal kingdom, and it is a matter for serious consideration whether it is dependent on speciation, the establishment of discrete species, or not.

The development of the body of every animal is regulated by a mechanism whose mode of action is still obscure but which is ultimately dependent on the character of the genes which lie in the chromosomes of its cells. The early stages of development have of late years been actively examined, but for our immediate purpose the proportional changes which take place in the post-embryonic development are of much greater importance, and their causation is at present even more obscure than that of embryonic development. But it is now obvious that growth is systematic, and proceeds regularly, so that it can be expressed by an equation. The nature of the equation is still uncertain, sometimes the growth of one organ with respect to that of the animal as a whole may appear disproportionate, it may in some cases be logarithmic, in others the curve may be a straight line not passing through the origin. For our immediate purpose all that is really necessary is to recognise that some relation, expressible in mathematical terms, does exist between the proportional sizes of the parts of an animal during its post-embryonic or post-larval growth. The implication of this is that the machinery which determines the character of the bodily changes which take place during the growth of an animal persists throughout its life, and that, if an animal becomes exceptionally large, its bodily proportions will fall on the same curve as that which represents the development of more normal members of the species. It is of course true, as Dr. Hammond has so clearly pointed out, that the effect of this mechanism may be altered, that bodily proportions may be changed to a very considerable extent by altering the plane of nutrition of the animal observed, that indeed gross changes in appearance may be produced by starvation followed by full feeding, or by the reciprocal treatment, during the growth of a pig or a cow, and the same phenomenon is evident in beetles and other insects, as Dr. Jordan pointed out to me. But these directly environmental effects, which are of course not heritable, are probably of no importance from the evolutionary standpoint which we are at present considering.

It is evident that the gene basis of such a mechanism regulating development must be of great elaboration, and it is conceivable, as is shown for example by such conditions as phocomelia and acromegaly, that it can readily be upset. Its persistence does indeed imply the maintenance in association of a large group of genes which are necessarily thus withdrawn, not from the occurrence of mutations, but from the utilisation of mutations in other evolutionary processes in which, as well as in the determination of bodily proportions, they may play a part. It seems evident, primarily from observations on the history of the Equidae, that, once established, such a proportion determining mechanism may be remarkably stable. The studies of Robb on the proportions of the skull in living and in fossil horses, and their further analysis by Simpson, seem to show that in that group the proportions change with size in a precisely similar manner during the growth of living horses, and throughout the entire series from *Hyracotherium* to *Equus*, during a period representing perhaps some seventeen million generations.

It is by no means unlikely that such a mechanism may control the development of structures which do not exist in the earliest animals whose growth was determined by it. The growth of the horns of *Titanotherium*, and of the deer, was

no doubt so determined. The early forms, which are small, possess no horns whatsoever, but these subsequently (and, in the case of Titanotheres ; in several different evolutionary stocks) make their appearance and then, with enlargement of the animals which lie later in the line of descent, exhibit a disproportionate enlargement. The potentiality of developing horns was always present but gained expression only on the attainment of some definite animal weight. The changes in proportion brought about by the action of such a mechanism are necessarily adaptive in that they are so ordered that the animal remains a working whole from youth to old age, and it seems evident that this adaptation, not to a specific environment, but to life itself, will be equally successful as the size of the animals in the series becomes steadily greater. Such a mechanism is almost certainly common to all members of a large taxonomic group although the constants in the equation which represents its effect may, and indeed will, differ in different stocks. Changes brought about in this way are necessarily orthogenetic in a strict sense, they appear to be those which Osborn regarded as due to allometry.

But, in addition to these allometric changes, there are others which proceed with some regularity in most of the stocks which have been investigated ; for example, in Perissodactyls a steady increase in size takes place in all families*. The weight of the animal determines its food consumption, other things being equal, and it has been shown, principally by Benedict, that the basal metabolism increases nearly proportionately to the surface area of the animal, whilst expenditure on general activity will depend directly on the animal's weight. Thus a large animal will eat more than a small one by an amount variable with the animal's activity but in any case exceeding the two-thirds power of its weight, which represents the area of surfaces. But in some cases, at any rate, the efficiency of grinding teeth varies with surface area, and it is thus necessary for a large animal to increase the relative area of the grinding surfaces of its cheek teeth. In all Perissodactyls this change is brought about during the early stages of evolution by modifications of the pattern of the pre-molars, which converts them into copies of the molars of the same series. This process of molarisation is done in different ways for different teeth, as Granger showed for the third and fourth upper pre-molars of the Eocene horses, and in different ways for the whole series in the various groups of Perissodactyls. The mechanism by which this change is brought about must therefore differ in kind from that which determines more normal bodily proportions, and it may well be explained on a natural selection hypothesis, for it is clearly not pre-determined.

It is, however, extraordinarily interesting to find that in the Artiodactyls, many of which lived lives comparable with those of the Perissodactyls, no such molarisation of pre-molars is normally found. In the most highly developed forms, such as the deer and antelopes, even the last pre-molar remains as a triangular tooth, very small in surface area in comparison with the molar that succeeds it. This applies to every group of Artiodactyl, to the pigs and hippopotamus as much as to the ruminants. Indeed, I believe only in one form, *Agriochoerus*, is a pre-molar (and only the last) molarised. It is very difficult to imagine why the Artiodactyls differ from the Perissodactyls in this way, for in animals of similar size the food requirements are essentially the same. It is possible that the ruminants, at any rate, escape the need for an increased grinding surface because the habit of rumination allows them to devote far more time during a day to mastication than is possible for horses, which must grind up the food whilst they are actually collecting and eating it. The only explanation which occurs to me is that some feature of the genetical make-up of Artiodactyls, analogous to that which in Perissodactyls enables the process

* The occurence of dwarfs, *Archaeohippus*, *Nannippus* and the Shetland pony does not really conflict with this statement.

of molarisation to be carried on, is, in Artiodactyls, so tied in with a fundamental mechanism which cannot be seriously modified without wide ranging and serious effects, that it cannot be made use of in evolutionary changes of the dentition.

In discussing the dentition of Perissodactyls I have not considered the special requirements arising as a result of changes in the normal food. In general plant materials secured by browsing on leaves and twigs seem to be easily and sufficiently broken up to become readily digested, but there is no doubt that grasses present different and more difficult problems. The silica contained in their cortex leads to heavy wear of the teeth which grind them up, and the hardness and small size of their stems and leaves make necessary the introduction of a cutting mechanism analagous to a pair of scissors, rather than bruising arrangements found in bunodont teeth. As the amount of work which can be done by a pair of scissors depends on the length of blade, it follows that with increasing size of a grass eating animal the length of the cutting edge (which is the enamel ridge on the crown of the tooth) must increase as fast as the square of a linear dimension, rather than as in a scale model. Thus the enamel pattern, especially of such late horses as *Hipparion* and the grass eating rhinoceros *Elasmotherium*, becomes exceedingly long and complexly folded. This increase is only in part foreshadowed by changes occurring in a pre-grass eating stage in smaller ancestors, and it cannot be attributed to the action of an established mechanism, although a Darwinian explanation is clearly appropriate.

None the less, the general character of the changes in the teeth of Perissodactyls does appear to proceed in a definite direction, and is thus orthogenetic in Osborn's sense, but the mechanism whereby they are brought into being obviously differs completely from that which determines the orthogenetic change in bodily proportions, and the apparent regularity of the development is imposed because the demands made upon the dentition (except those arising only in relation to the grass eating habit) remain the same, and the modifications in structure observed are rendered necessary primarily by that increase in size which leads to modification of bodily proportions.

Thus we are drawn to the consideration of what factors have led to the increase in size which is the determining factor in so many of the evolutionary changes of mammals. It may be supposed that the lower the food requirements of an animal per kilogram of its bodily weight, the more successful it will be and the greater the possible range of its activities. But the observation that the increase of basal metabolism with increase in size is not proportionate to the increase in weight, but more nearly to the increase in surface area of an animal, implies that the thermodynamic efficiency of a large animal is always greater than that of a small one of the same species, or indeed of any rather closely related form. In fact, a good large dairy cow is potentially more economical than an equally good small one of equal milk yield per pound of body weight.

The changes we have just been considering are thus adaptive ; they enable a large animal to live as successfully as a small one. In that a large animal is thermodynamically more efficient than a small one, they enable this life to be carried on at a lower cost in food intake, and a large animal is less subject to the attacks of predators than is a small one ; but an adaptation of this kind differs very greatly in character from that precise fitting of an individual to its environment which was, I think, in Darwin's mind when he discussed the mechanism of evolution. They differ in that one is restricted to a species whilst the other series of changes is common to the members of a number of related but independent stocks, and it is therefore necessary to discuss whether or not major evolution is dependent on speciation ; that is in effect on the appearance of bars to fertilisation or not. The problem is a difficult one for at present there is no case in which the immediate ancestry of an animal which has been used in breeding experiments is known, and I can think of few things potentially more

valuable than a study of the genetics of rodents whose geological history is capable of determination. The genus *Siphneus*, whose late Tertiary history has been so well described by Father Teilhard, presents one possibility, but I feel that thorough study of recent and fossil British voles might provide the opportunity for an invaluable piece of work.

Many of the series illustrating the history of marine invertebrates over a comparatively short period, like that of the Micrasters or of *Zaphrentis*, suggest that the changes observed go on in the population as a whole, that they reflect corresponding changes in the distribution in the population of genes which can have been brought about accidentally (as Sewell Wright has shown) even without any direction from natural selection in the case of small populations, and which would, I think, occur under the influence of natural selection even without the introduction of an interspecific sterility, and hence the production of new species. But such a change would depend, I think, on a persistence of definite ecological conditions throughout the series, and also of habit in the animals considered.

This matter of the persistence of habit is, I feel, of great importance and has perhaps been inadequately considered. It is clear that in some cases habit, as represented by instinctive behaviour, is as dependant as are morphological qualities on the hereditary mechanism. The elaborate series of activities which birds display in building nests must clearly be so determined, for a bird cannot know from observation of the nest in which it was hatched the way in which that nest was originally built by its mother. None the less, the nest it will produce in its first nesting season will be of the type appropriate to its species. If then such instinctive behaviour be determined by a hereditary mechanism, it will, in so far as this mechanism persists, be itself repeated generation after generation for a time of the same order of extent as the morphological characters determined by other parts of the mechanism. But mutations and chromosomal changes of a kind which establish the sterility which characterises a species, or bring about changes in structure, will affect it in corresponding ways. The animals so changed may be expected to take up new modes of life and may, by the action of natural selection, develop new adaptations, but it seems evident that habits which are not directly imposed by any properties of the environment may persist for very long periods.

An example may conveniently be found among the Plesiosaurs. These are large marine reptiles found in shallow seas all over the world continuously from the Lower Lias to the Upper Cretaceous. At all these horizons several types occur which fall, not very accurately, into two groups—the small-headed, very long-necked form and the large-headed, short-necked one. In the Lower Lias the long neck never contains more than 35 vertebrae, the short neck never fewer than 27, whilst in the Upper Cretaceous the long-necked forms may have 76 cervical vertebrae and the short-necked forms only 11. Thus, in this respect, the two groups diverge more and more widely, and rather inadequate evidence shows that at intervening periods the differences between them were less extreme. Throughout their whole history each of these two groups of Plesiosaurs is complex, minor evolutionary lines may be recognised and in some cases followed within them, but they are always found side by side, living in the same seas and having available the same potential food. The difference between them is evidently related to variations in feeding habits. In the small-headed, long-necked forms the head, at an extreme, may be 33 cms. long in an animal measuring 806 cms. (the smallest head in proportion to the body known in the entire animal kingdom) whilst in the large-headed type, *Trinacromerium*, the skull is as long as the neck, and is one-fifth of the entire length, against one twenty-fifth in *Elasmosaurus*. Such gross disproportion clearly implies an entirely different food. The small-headed forms possess an irregular series of long, slender, sharp-pointed teeth which may be worn smooth but are never

truncated by wear. They are entirely suited to the capture of small, quick moving animals, fishes and cephalopods, and remains of fish have indeed been found within the ribs of fossil Plesiosaurs. The large-headed Plesiosaurs have teeth which may be extraordinarily massive, as in *Pleiosaurus*, with short crowns not seldom worn down to mere stumps. They obviously ate large animals with powerful bones capable of causing this wear on the teeth.

An analysis of the shoulder girdles and pectoral limbs of these forms suggested to my mind that the series of structural changes, which take place between the beginning and the end of the story, are of such a kind that the speed of movement of the long-necked forms directly through the water must have been reduced, whilst that of the short-necked forms increased, and that the long-necked forms developed a power of swinging the head laterally through a large arc and rapidly, whilst the neck of the large-headed forms becomes less and less flexible, and no provision is made for rapid lateral movements of the head. The implication is that the long-necked forms caught their relatively small and rapidly moving prey by guile, by rapid lateral flicks of the head, whilst the members of the other group ran down the large animals on which they fed by sheer speed, capturing them in their enormous mouth when they had overtaken them. It is evident that these changes are adaptive, but that they are adaptations to feeding habits selected from a very much greater range of possibilities, and that these habits must have persisted from beginning to end of the whole history of the two stocks, for only so can the changes of structure, which have every appearance of arising under the influence of natural selection, have been brought about. Thus we have, I think, a clear illustration that habits may be as persistent as any morphological quality.

The cases I have so far considered seem to show that there may be considerable differences between the processes of micro- and macro-evolution, between the establishment of sub-species, and of species, and those more fundamental changes common to related stocks within a relatively large group, which ultimately bring about large changes in proportion of parts and other morphological qualities of animals, and it is important to consider whether or not there be any genetic changes of a still different quality.

One example, which is now well established and very widespread, seems to be of such a nature. It is known from abundant evidence that the primitive members of many groups of fishes and of fish-like craniates have remarkably complete ossification of their neural cranium. In Cephalaspids, Arthrodeirs, Osteolepids, Coelacanths, Dipnoi and Palaeoniscids the early members all have singularly well-ossified brain cases, and in each of these groups it seems evident that the amount of this cartilage bone tends to be reduced with time until it may almost cease to appear. In each case the change may be put in the form that the time of appearance of cartilage bone in the neural cranium, and usually also in other parts of the skeleton, comes to be placed later and later in the life of the animal, so that the living *Ceratodus* and the living sturgeons and spoonbills only develop bone in their neural cranium when they are old, even fully mature individuals completely lacking it. The phenomenon is a very striking one, and it is remarkable that the delay in ossification seems to occur without reference to the habits of the fish. The Cephalaspids, Osteolepids and Dipnoi are at least predominantly fresh-water forms, but the Palaeoniscids in their later stages are usually marine, and so are the Coelacanths, and thus it is difficult to believe that any lack of calcium is responsible for the change, nor can the phosphatase mechanism be deficient, for sturgeons, at any rate, have a well-developed bony skull roof. Indeed, the whole machinery of the change is obscure, though it may perhaps be related to the delay in the attainment of sexual maturity, found at least in the Dipnoi and the sturgeons.

This steady decrease in cartilage bone occurs in a typical and very recognisable manner amongst the Labyrinthodonts, and in some of the other divisions of the Amphibia. It may, indeed, be common to them all. But the Labyrinthodonts present another secular change which proceeds in a similar manner ; this is a flattening, beginning at the anterior end of the head and progressing backward along the body until it may extend as far as the hind legs, though never, I think, showing itself in the tail. These two series of changes in Amphibia, which are exhibited in that group whether they be aquatic or terrestrial in habit, at various stages of their careers, raise many mechanical difficulties which must be met if the animal is to remain a functional whole, capable of making movements of its jaws, head and body without subjecting the skeleton to stresses which it is not competent to support. The more immediately evident evolutionary changes in the skull and skeleton of Labyrinthodonts represent consequential modifications, brought about in all probability under the control of natural selection, which fit the animal's skeleton to withstand the stresses to which it is subjected. These changes cannot be pre-determined because they are brought about by somewhat different routes in different lines of descent.

I have found it impossible to interpret the fundamental changes—the decline of cartilage bone and the depression of the anterior part of the body—on any theory of external environmental influence, either direct or through natural selection. The changes imply modifications in the hereditary mechanism which determines development. In a sense, the condition of phocomelia, exemplified by the Scotch Dumpy fowl, provides a parallel to a reduction in cartilage bone, occurring without any corresponding change in membrane bones. In the fowl the condition depends on a single, recessive, semi-lethal gene, whilst in the amphibia and the fishes the change is gradual, finally working up to a maximum. It cannot be the work of a single gene and may indeed, depend on a steady retardation in the achievement of maturity.

The very brief survey of evolutionary methods set out above shows, I think, how very varied are the actual processes of evolution, and how much of the great change which is seen to occur in the evolution of a large group of animals is of a kind unlike that which brings about the differentiations of species, and of the sub-species contained within them. Sub-species may very often result from what Sewell Wright called drift. They may represent an accidental modification of the proportions in which genes and their mutations exist in a population brought about by chance, though necessarily controlled by natural selection in that the animals forming the sub-species must be capable of life in the circumstances in which they find themselves. In some cases what appears to be a direct adaptation, as of a parasite to some specific host, may be, and perhaps always is, the result of a chance mutation, or indeed of a new opportunity of infestation presented by an enlargement of the geographical range of a parasite or of a potential host. In fact pre-adaptation does indeed occur, but does so accidentally without reference to possibilities of utilisation. The establishment of new species, which means in fact the setting up of a bar to fertilisation between different members of what was originally the same species, is probably very often (or even usually) the result of an accidental chromosomal change brought about by radiation, or by some other analogous cause.

But the main evolution, which brings about large structural differences whose development is often visible throughout a large division of the animal kingdom over a prolonged period of thousands or even millions of generations, seems to be something different. In many cases it may merely represent the working out of individual development under the control of a hereditary mechanism which secures that, throughout the increase in size of an individual, the proportions of the various parts of the skeleton, and of other organs of the body, change in such a way that the animal at every weight remains a workable living being.

If, during the course of evolution, individuals whose development is determined by such a mechanism become larger under the influence of natural selection, then their proportions will necessarily change, so that the large animals which ultimately arise within the evolutionary series may differ greatly in proportion from their small forerunners, and altogether new structures, like the horns of Titanotheres or deer, may appear and undergo a spectacular development without any change in the developmental mechanism which controls the growth of each individual. Such an evolutionary series will exhibit in perfection the phenomenon of orthogenesis. But there are other cases in which an apparent orthogenesis has a different basis; for example all Perissodactyls exhibit a molarization of pre-molar teeth, but they do so in ways which differ so much as to make it impossible that the changes represent the working out of a pre-existing developmental mechanism. They can be explained on a natural selection basis, the adaptations being not to external circumstances but to the functional requirements of the animal itself, requirements which change in their magnitude with increase in absolute size.

There are a very few rare cases in which evolutionary changes of magnitude, common to all stocks lying within large groups of the animal kingdom, exhibit an orthogenetic trend which cannot be explained by natural selection, and which it is very difficult to believe are produced as a result of the working-out of a developmental mechanism as in 'typical' orthogenesis. The most striking of these is the delay in the time of appearance of cartilage bone, especially in the head of very many diverse groups of lower vertebrates. Here the facts are well established, but their significance is unknown to me. I have found it impossible to imagine any mechanism which can have brought the basal changes about.

It is evident that evolution, depending as it does on an immense series of contingencies extending through past time, must depend on an infinite number of accidents, lucky accidents in that they have produced forms capable of maintaining themselves under the world conditions into which the animals displaying them were born. The whole story is one of improbabilities, but the time available—some two thousand million years, of which only five hundred million are represented by fossil materials—is so vast, the number of individuals involved so enormous, and the number of gametes they have produced so inconceivably great, that the rate of appearance of mutations and other chromosomal changes, relatively slow though it be, and it is after all measurable experimentally, is amply sufficient to provide the materials which, preserved by natural selection, have enabled the animal and plant kingdoms as we know them today to have come into existence.

PROCEEDINGS OF THE GENERAL MEETING ON

13 May 1948

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meetings, held on Thursday, 22 April and 29 April 1948, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. H. N. Ridley, C.M.G., Dr. Hugh Scott and Messrs. G. Bell & Sons, Ltd.

The following Fellows signed the Obligation in the Roll and Charter Book, and were Admitted Fellows :—Mr. Charles Lionel Duddington, M.A., Dr. Richard John Harrison, M.A., M.B., Mr. Abdus Sattar Khan, M.Sc., Dr. Ronald Gordon

Newton, Mr. Joseph Henry Garfield Peterken, Mr. Arthur Alfred Prestwich, Dr. John Philip Harding, Mr. Paul Octave Wiehe, Mr. Harvey Goodall Langham, Dr. Charles George Maurice de Worms.

The following papers were read in title :—

'Some Roundworms and Flatworms from the West Indies and Surinam.—III. Trematodes'. By STEPHEN PRUDHOE. [To be printed in the Journal, Zoology.]

'Some Roundworms and Flatworms from the West Indies and Surinam.—IV. Land Planarians'. By STEPHEN PRUDHOE. [To be printed in the Journal, Zoology.]

'On the Polychaeta collected by Mr. J. Colman at St. Helena'. By J. H. DAY, Ph.D. [To be printed in the Journal, Zoology.]

'Tropical Fungi.—III. New Species and revisions'. By C. G. HANSFORD, M.A., F.L.S. [Printed in full, p. 116.]

'The Morphology of the head of *Gymnarchus*'. By M. OMARKHAN, M.Sc. [To be printed in the Journal, Zoology.]

The following communications were read and discussed :—

A DISCUSSION ON THE ORIENTATION OF BIRDS ON MIGRATORY AND HOMING FLIGHTS.

Dr. W. H. THORPE. Recent Biological Evidence for the Methods of Bird Orientation.

Dr. D. H. WILKINSON. The Physical Data theoretically available for Bird Navigation in unknown country.

(The following also took part in the discussion :—Prof. Wojtusiak (read by Mr. H. W. Parker), Dr. A. Landsborough Thomson, C.B., O.B.E., Prof. V. C. Wynne-Edwards, Mr. James Fisher, Mr. B. W. Tucker, Dr. M. H. Pirenne, Dr. R. G. Newton and the President ; Dr. Thorpe replied.)

A DISCUSSION ON THE ORIENTATION OF BIRDS ON MIGRATORY AND HOMING FLIGHTS

RECENT BIOLOGICAL EVIDENCE FOR THE METHODS OF BIRD ORIENTATION

By Dr. W. H. THORPE.

There are three distinct aspects of the bird orientation problem, and I propose to consider how far these can be explained in terms of known senses and sense organs, and in so doing to review the more important papers on the subject published since 1940. My indebtedness to the earlier writings of Dr. A. Landsborough Thomson will be obvious to all.

I think these three aspects of the bird orientation problem are :—(1) Knowing what direction in which to start, (2) Maintaining direction once started even though unfamiliar with the ground and under bad conditions, (3) Recognizing the goal when reached. It might be convenient to take these in reverse order,

I. Recognition of Goal.

This point need not detain us very long, although it is a very interesting one and would provide a good subject for discussion were it not rather outside the field of to-day's programme. Moreover, I do not think the recognition of the goal demands any sense organ, or sensory or psychological ability not already fairly well established as occurring in birds. There is plenty of evidence that migrating birds will return year after year to breed at the same spot. Birds are known to have good visual memory and there seems no reasonable doubt that they recognize their breeding areas by means of familiar landmarks. Moreover, it seems quite evident that many birds can recognize by sight the territory in which they were reared, and for a number of species there is evidence of a tendency for young birds to return to breed in the general area of natality (Farner, 1945; Werth, 1947). In addition to this, one can safely assume that, quite apart from the recognition of a particular locality, birds can recognize the right *type* of environment for themselves. If this were not so, every year one would find birds trying unsuccessfully to breed in all sorts of unsuitable places. This recognition of an environmental type may be very largely the result of experience, but it is in line with the modern concept of instinctive behaviour (Thorpe, 1948) to assume that there may be an innate hereditary, primarily visual recognition of the right type of environment. Such an ability would seem to be astonishing enough and might at first sight appear to throw an overwhelming burden on the hereditary mechanism. But in reality it perhaps is no more remarkable than the ability of a hand-reared duck to recognize instinctively at first sight the drake of its species, or of hand-reared birds to build correctly at the first attempt the elaborate nest characteristic of the species. There remains the problem of outward flight to winter quarters. Experience will guide older birds and the young birds can associate with them. Even if the young birds travel alone after their elders have left, and even if there is no innate recognition of suitable winter quarters, they will be able (provided they can travel in the right general direction) to identify their winter quarters, perhaps by climatic and ecological data, perhaps by seeing the elders of their species already there.

II. Maintenance of Direction once started.

The sense organs and visual memory of birds being what they are, the maintenance of direction is obviously no problem when the bird is flying over familiar territory with numerous landmarks by day in good weather. But these ideal conditions are often lacking. Much migration (*e. g.* of waders) takes place at night. This seems particularly to be so when the flight involves crossing an environment inhospitable or abnormal for the species ; for example, when small passerines have to fly over the sea or ducks over the land. (It would be interesting to know to what extent small passerines migrate over land by night. I suspect very little : but perhaps Dr. Landsborough Thomson can give us some information.) It is well known that birds tend to wait for anti-cyclonic conditions before starting on sea crossings. There is abundant evidence that they tend to get lost in heavy rain, and that the well-known attraction to lighthouses is a sign that they are lost ; this dazzle by lighthouses only seems to happen when a sudden rush of birds has been overtaken by bad weather.

The next question is, how far can visual cues be used at night ? Bird vision is good, not as a rule because of extreme acuity, but because of phenomenal power of fixation by the foveae (Pumphrey, 1948). There is good evidence that the night vision of many diurnal birds is poor by human standards ; many, indeed, may be almost night-blind. I know of no satisfactory evidence of infra-red vision in birds, not even in owls. (Hecht and Pirenne, 1940.) If it is lacking in owls, I think, it is most unlikely that it is present in other birds, but it

is perhaps reasonable to assume that on moonlight, but not on starlight, nights, passerine and other birds could see rivers, lakes and coast-lines, and the silhouettes of hills, mountains, etc.

Then there is the question of light-compass orientation. I think the maintenance of direction by the moon is not improbable. Probably birds have a good time sense. Many insects, ants, bees, etc., can maintain direction by keeping a constant angle to the sun's rays, continually compensating by time sense and by use of landmarks for the movement of the sun, and it seems not unreasonable to assume that birds can do as well as insects in this respect and can maintain direction to some extent by the sun or moon. When flying over the sea they could not of course compensate for wind drift by sight of the sun or moon alone, but they might perhaps be able to do so with the aid of a wave pattern. But what can they do on nights when there is no moon? Orientation by stars does not seem impossible to conceive. I do not, of course, suggest that the bird can sight on the Pole Star. But I would not rule out the possibility of maintaining a general direction for a few hours by reference to a conspicuous star pattern. Birds have an excellent form vision and memory, and by making the brighter stars stand out more it is conceivable that this poor night vision might help in making a star pattern more conspicuous. But here again if compensation for wind drift is possible at all it can only be with the aid afforded by sight of a wave pattern when over the sea (or of landscape when over the land). Such compensation need not perhaps be very accurate for, after all, when flying over the sea, the great majority of birds do not have to hit on a particular point; as long as they reach some part of the opposite coast-line it will probably suffice.

But how can birds orient themselves at night during periods when the moon is absent, when the skies are overcast and when landmarks and wave patterns are invisible? In this connection, I think, we want to know very much more than we do about the effect of overcast skies on migration. I assume that even at sea, skies are much less uniformly overcast at night than by day. What above all we want to know is how much migration takes place on moonless nights with heavily overcast skies. I suspect the answer may be none. Perhaps subsequent speakers will be able to give us some information on this point. Even if birds were highly sensitive to magnetic and Coriolis forces, it seems quite impossible that they could navigate over the sea under such conditions, for estimation of 'land speed' maintenance of constant height would obviously be out of the question.

III. How do Birds know initially which Direction to take?

If we are right in concluding that known sense organs and senses are adequate for normal direction keeping, then, since migration is very often social, we can also look for a solution along the same lines, for there will be older and more experienced birds to give the initial direction and guide the flock to some extent. It is true that in some cases young birds leave after their parents and travel separately, but that is perhaps not an insuperable difficulty. Although it has been made quite clear by the experiments of Rowan, Rüppell and Schüz that young birds can in fact find their approximate direction South without guidance, it has to be noted, as Griffin and Hock (1948) point out, that all the experiments of these workers were carried out North of 50° latitude where the sun is always perceptibly South of the Zenith. Perhaps all we need to assume is that the young birds in the Autumn with regressing gonads have a tendency to fly in the general direction of the sun. That might seem to be a remarkable achievement, but it is surely no more remarkable than many other inherent tendencies of animals, and in the present state of our knowledge is certainly preferable to more recondite theories. The real problem emerges when we come to consider homing

experiments with wild birds and how far they necessitate postulating an innate sense of direction. Some evidence for a ' sense of direction ' of a kind is supplied by the recent work of Rüppell (1944) on the homing of the hooded crow (*Corvus c. corax*). He took very great care in planning the experiments so as to make sure that the knowledge that these birds had been released was very widespread over the whole of the part of Europe concerned. All reasonable precautions seem to have been taken against observational bias and I think this can safely be ruled out as an explanation of the results. The study of the hooded-crow population of the southern shores of the Baltic Sea and of the migratory movements of this population has been going on for a very long time, so that as a basis for Rüppell's experiments there is an unusually complete body of information about the movements of the bird population concerned, and it is well established that the crows which winter on the German coastal region of the Baltic west of Rossitten and in the northern part of Germany migrate in summer to breed in the general area of Lithuania, Latvia, Esthonia and Finland. Rüppell captured 900 first year birds on their spring migration near Rossitten and transported them to Flensburg in Denmark. Returns of the experimental birds made during the first summer showed that these had continued to fly in a north-easterly direction roughly parallel to the main migratory movement thus arriving in various parts of southern Sweden and north-eastern Denmark. Only one of these birds is recorded as getting back to its normal summer home, *i. e.* Lithuania, that same season and that appears to have been an older bird which was included in error among the first year birds used for experiment. Four birds, however, reached the island of Gotland in their first summer. While most of these birds released at Flensburg returned to breed in subsequent years in their new summer quarters in Sweden and Denmark, there were a few exceptional birds that got back to their original region of summer distribution, but the significant fact emerged that these also were not first year birds but individuals which had been captured at a greater age, and there is thus reason for thinking that it was the previous experience of these older birds which enabled them to navigate so as to correct the experimental displacement which they had undergone. The winter distribution of the experimental birds is also interesting. They appear to have followed in their autumn migration roughly the same route as the normal bird population of their new home. Several thus got to England. It seems clear, therefore, that there was a general tendency to keep their new parallel line in the migrations of succeeding years both in summer and in winter. The obvious objection to considering these results as very significant is that the hooded crow migrates largely by day and in very large numbers in this area. It is, therefore, quite reasonable to suppose that experimental birds were merely following other birds from the countries to which they had been moved. This explanation is, however, ruled out by another experiment in which birds were transported to Essen and Frankfurt. The birds taken to Frankfurt could not have had the guidance of other individuals of their kind, for Frankfurt is outside the normal range of the species. Yet they still kept a north-easterly direction. It is true that results with the Essen and Frankfurt birds were not as good as those obtained with previous releases ; but in view of the great precautions Rüppell took to ensure that the observations were not biassed, we must, I think, conclude that his figures give a real picture of the line taken by the Frankfurt birds.

Since hooded crows are day migrants, Rüppell's results can however be accounted for on the basis of a tendency to fly in a certain direction with reference to the sun at a certain time of the year. It is perhaps legitimate to describe this as ' an innate sense of direction ', but I do not think it is necessary to postulate any mysterious method of orientation, the visual sense apparently being adequate to account for the results.

The homing abilities of many wild birds are well known—*e. g.* gulls, terns

petrels, gannets, starlings, swallows and martins ; but I think the great majority of experiments with these birds can be accounted for on the basis of considerable previous knowledge of the country. If the bird has not been taken out of familiar territory, it can return by means of known landmarks. The only experiments which are really crucial are those in which we can be virtually certain that the birds have not been over the ground before—Rüppell's swallows, for instance (Rüppell, 1934 36 and 37)—and especially those in which the birds are taken right outside the range of the species, such as Watson and Lashley's (1915) terns and Lack and Lockley's (1938) shearwaters.

Those who have read Griffin's (1944) review will be familiar with his diagram which shows what can be accounted for on the theories of random radial scatter and spiral exploration. Fig. 1 gives a modified form of this diagram.

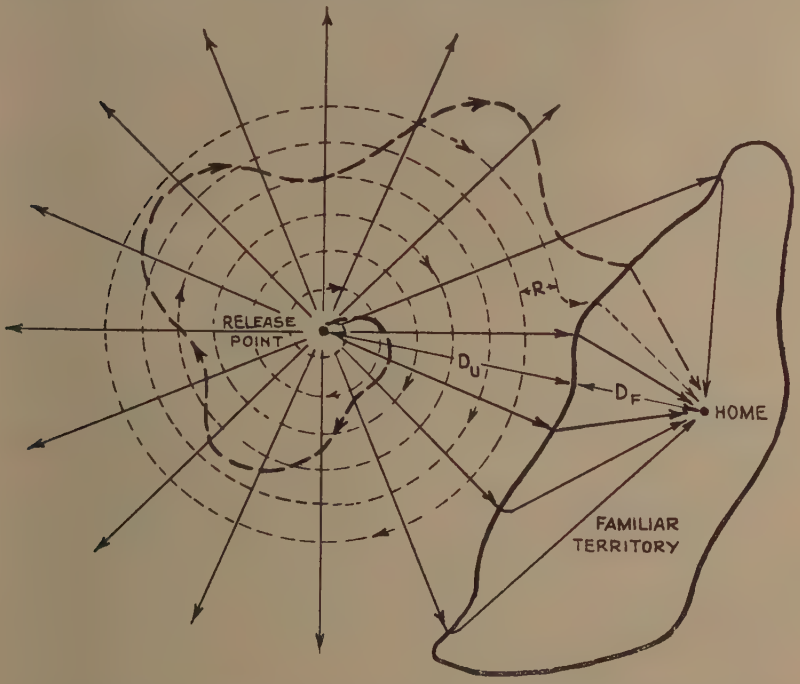

Fig. 1.—Hypothetical flight-paths of birds homing by means of random radial scattering (solid lines) and spiral exploration (broken lines). (Modified from Griffin, 1944.)

In this diagrammatic instance, five out of sixteen birds reached home by means of radial scattering, flying courses 1·03, 1·04, 1·18, 1·67 and 1·71 times the straight line distance $Df + D_u$. The bird homing by close spiral exploration (fine broken line) would have flown approximately 13·3 times the straight line distance.

Suppose that the irregular area shown on fig. 1 labelled ' familiar territory ' represents country known to the individuals of a colony of birds nesting at the point marked ' home '. A group of these birds is taken away to a release point in unknown country. On the supposition that these birds scatter at random and that they fly a straight course, one would still get about 25 per cent. of them reaching known territory within a reasonable time. Once within the known territory they can fly home on a more or less direct course guided by visual landmarks. If, therefore, in such a case where the relative distances are

approximately as indicated on the diagram, the recoveries from an unknown territory are of the order of 25 per cent. or less, we need not assume any innate sense of direction. If now, the birds (not having an accurate directional sense) are to be *sure* of striking a given point, they must fly in a close spiral as indicated by the fine broken line ; the distance *R* being the range of vision. This would ensure their reaching home ultimately ; even if they only knew the immediate surroundings of their nest, but would, of course, take a long time. Even if the birds knew the area marked ' familiar territory ' on the diagram, they would, using this close spiral course, have to fly approximately 13·3 times the straight line distance. It is not very easy to imagine how the birds would orientate themselves on such a course, although we must beware of assuming that they could not do so. But clearly in the case indicated, with a considerable area of familiar territory, the birds need not fly a close spiral but can afford to travel on a much wider and more erratic spiral or helical course (as shown by the coarse broken line) and still have a very good chance indeed of reaching the known area. There are thus three possibilities, and we must be careful to rule out all of them before assuming the existence of some innate sense of direction.

It is, therefore, very important to observe the percentage of return and the average speed of return, and we find that these usually drop steadily with increasing distance. I think Griffin has shown fairly conclusively that in nearly all these cases in which birds are transported into unfamiliar territory, the percentage of recoveries and speed of returns are consistent with random scattering or spiral exploration.

We must not overlook an important class of clues to which Griffin (1944) has referred, namely the clues provided by the persistence of characteristic air masses of fairly constant temperature and humidity. These, coupled with the knowledge of the general line of rivers and coastline and of the winds which are constant for a particular season or particular time of day, may provide a great deal of information to a migrating bird which it is difficult for us to imagine. An experienced glider pilot knows well how much information air conditions can provide—information which the mere land lubber would never guess was available.

There is, of course, a large amount of information of a kind about homing orientation available from the records of homing pigeon racing. This has been discussed extensively by O. and K. Heinroth (1941), Knieriem (1943) and Koehler (1943). It is difficult in many cases to know exactly how much reliance to place on such data, and I hope that Mr. Matthews, who has gone into this literature more thoroughly than I have, will give us his conclusions about it. I think, however, it can be said that initial training steps must always be small and very cautious. The birds are usually released at the same time of day and in the same direction from the home, but even with all these precautions, pigeon fanciers suffer initially a high proportion of losses. Then when the good homers have been selected out and the birds have been well trained, it is possible sometimes to increase substantially the distance to be flown (not necessarily in the same direction), and the birds will fly home at about the same speed. It must, however, be borne in mind :—

(1) That homing pigeons are usually released in groups, some birds of which may have had more extensive experience.

(2) That these highly selected homers are undoubtedly extremely quick at exploration and are quick flyers.

(3) Since they are well fed before release, they do not have to stop *en route* to feed.

This last point helps to explain why such high speeds may be recorded in favourable conditions, for instance up to 1,000 miles per day. I think the

implications of such results are that the previous flights of the birds have probably made them familiar with a much greater area than we might expect.

It seems probable then that all pigeon results are explicable on the basis of good vision, quick learning of landmarks and rapid and efficient methods of good exploration.

The crucial point, of course, in all these cases, and on which we need information almost more than any other, is what flight path is actually taken. Such evidence is hard to come by. In these homing experiments birds on release sometimes scatter, apparently at random, and sometimes fly in spirals. Griffin has done some valuable pioneer work in attempting to follow by helicopter the route actually taken by sea birds when released over the land in unknown territory, and Griffin and Hock have recently (1948) published an account of some similar experiments with Gannets (*Morus bassanus*.) The birds were taken from their home on an island in the Gulf of St. Lawrence and were released over land at about 100 miles from the coast between the St. Lawrence River and the Bay of Fundy. It was found possible to follow them for a considerable distance, in some instances more than 100 miles—and returns gave no suggestion at all that the birds had any idea in which direction to go. The initial direction taken appears to have been more or less random, with some suggestion of spiralling and, in some cases, fairly long stretches of straight flight. The actual paths followed suggest exploration rather than any innate sense of direction. The control experiment gave no suggestion that the presence of the aeroplane was affecting the birds and it seemed to have no detrimental effect on their homing ability. Approximately 60 per cent. of both experimental and control birds ultimately reached home at an average overall speed of 99 miles per day.

There is, however, some evidence that birds when released in unfamiliar territory will, on occasion, take a straight route home, but the evidence is not very extensive. In Rüppell's experiments with starlings (*Sturnus vulgaris* L.) (Rüppell, 1935–37), three birds were recovered on the direct route home. Two of them may have been in familiar country, but the third almost certainly was not. One or two of the Herring Gulls (*Larus argentatus*) used in Griffin's earlier experiments (Griffin, 1943), seem to have followed a fairly direct course, and one bird which spent some days at Toronto on its way home must eventually have flown home fairly directly. There are a few other exceptional results :—one of Griffin's, Leach's Petrels (*Oceanodroma leucorrhoa*) (Griffin, 1943) apparently took a short cut over land, and the famous Manx Shearwater (*Puffinus p. puffinus*) sent by Lack and Lockley (1938) from Skokholm to Venice cannot have had much time for exploration on its journey home at the average speed of 260 miles a day, and these authors had some other less striking but, nevertheless, very remarkable results. To sum up, there are quite a number of results of homing experiments which are puzzling enough to warrant us looking carefully to see what other factors may be available for orientation of homing birds.

One should perhaps say something about the possibility of orientation by kinaesthetic receptors. I agree with Griffin that the accuracy and complexity of labyrinth memory required to make this theory feasible would be so astounding as to render almost any other alternative preferable. Moreover, the experimental evidence against it is considerable. For instance, pigeons and some other birds have been transported in rotating cages under anaesthesia and after injury to the semi-circular canals (Huizinga, 1935), but without any apparent serious effect on the return journey. Yet none of these refutations can be regarded as absolutely conclusive since in no case were the birds shipped far enough to be certainly outside familiar territory.

The theory that homing birds are able to orientate themselves by means of some forms of magnetic or electrical receptors has frequently been put forward, but experiments in which birds have been exposed to magnetic fields have failed

to give any evidence of sensitivity, and it has not so far proved possible to train birds to respond to a magnetic field. But this whole side of the problem of bird orientation has been revived by the suggestion of Ising (1945) that the Coriolis force—a gravitational force generated in this case by the rotation of the earth—might be perceived by birds by means of the semi-circular canals and thus confer latitudinal and directional sense. Ising's work was purely theoretical involving no experiments on the bird itself. It has already been critically discussed (Thorpe and Wilkinson, 1947) and will be dealt with later this afternoon by Dr. Wilkinson.

Finally, there is the work of Yeagley (1947) carried out in America between 1942 and 1945. This work was based on the assumption that homing pigeons are sensitive to the effect of motion through the vertical components of the earth's magnetic field and to the effort exerted to overcome the Coriolis forces due to the earth's rotation. Each of these influences provides a set of lines joining points of equal intensity and which together form a navigational gridwork. The theory is that by correlating its instantaneous land speed with the two effects, a bird can fly to its home which is unique a point in this gridwork, or to related conjugate points existing in the gridwork at a position other than its home. Yeagley conceived the ingenious idea of having mobile lofts and of transporting these and their contained pigeons in such a manner as to test the theory that ' if a bird locates its home by navigating to the intersection of the proper magnetic vertical and the proper latitude, he should as readily navigate to the conjugate point as to his home if released nearer the former '. The conjugate point was situated at Kearney in Nebraska. Pigeons were trained at State College, Pennsylvania, to return to a conspicuous mobile loft from up to 70 miles in various directions. Loft and pigeons were then transported to Nebraska and the pigeons released at distances between 25 and 75 miles from the conjugate point. Yeagley's paper is so constructed that information on many essential points is either lacking altogether, or at best can only be extracted by considerable labour combined with the study of large scale maps of Nebraska and other states. I am very much indebted to Mr. G. V. T. Matthews for working out some of the details of Yeagley's results and thus giving us a much clearer idea than is otherwise obtainable of what the experiments actually amount to. Yeagley does not subject his data to any statistical analysis, nor are enough details given to enable any satisfactory assessment to be made by others ; but such statistical significance as the results appear to possess may be accounted for by observational bias. The experiments involved transporting and setting up large mobile lofts which were rendered as conspicuous as possible to increase the chance of the pigeons finding them, although far less than one per cent. of the birds succeeded in doing so. Thus, for ' returns ' the experimenters had to rely on the birds being found and records sent in by pigeon fanciers, farmers and others up and down the country. It seems only reasonable to assume that large-scale experiments of this kind with the lofts set up in the region where the birds are expected to return were likely to attract a good deal of local interest and attention. Unless great care had been taken to counteract the effect on the returns of this local interest by ensuring that the birds were looked for equally intensively in the area where they were not expected to appear, the results are open to great suspicion, No mention is made in Professor Yeagley's paper of any precautions having been taken in this connection, and so it must be assumed that they were not, in fact, taken. The mobile lofts were large structures painted bright yellow, surmounted by a five-foot observation balloon attached by 150 feet of cable. These very conspicuous objects were towed about the countryside in the course of the experiments. Local interest and excitement can easily be imagined, particularly when we consider that the first loft was set up on the fairground of Kearney, Nebraska, and unless great precautions were taken, news of the

experiments must quickly have been spread about. In the absence of any such precautions any results must be received with great caution. A more satisfactory method would have been to have had a ring or concentric rings of mobile lofts grouped round the release points so that there was an even chance of picking up the birds in any direction. There is also some ambiguity about the way in which the birds were treated. The main experiments in Nebraska are described as the 'first' and 'second' Kearney experiments. In the first experiments 98 birds were released and 44 recovered. The weather conditions were, on the whole, not favourable. 78 of the birds were released not more than 50 miles away, 17 were released at 70 miles and 3 at over 100 miles. Initial directions of the flights are not given, and the releases were presumably single, but no information is given on this point. It is, however, stated that 'birds were allowed to rest one day to acclimatize themselves to their surroundings'. The exact meaning of this phrase is not clear. A different phrase is used in the account of other experiments. In the second Kearney experiment 200 birds were released and 32 per cent. eventually recovered. None of these birds found the lofts although one came to Kearney. These birds were released in groups of 3 or 5—details not given—which would tend to decrease any apparent significance of the results. These birds were kept at Kearney before the experiment 'one day for resting the birds'. The 'East-West' experiment is particularly interesting and also calls for some comment. According to theory, if birds were released in the Illinois region south of Lake Michigan, they should not be able to home successfully because this is an 'area of tangency' where the two sets of lines composing the gridwork run approximately parallel and should consequently be useless for navigation. Accordingly, the birds trained in Pennsylvania were released in three lots :—

(1) Birds released in Iowa and Nebraska well west of the line of tangency.

(2) Birds released in Illinois or Indiana in the line of tangency.

(3) Birds released east of Lake Michigan in Pennsylvania and Ohio.

The first group were expected to fly towards the conjugate point at Kearney. The second should have shown no ability to direct their flight ; while the third group were expected to home in the direction of State College, Pennsylvania. In all groups there seems to have been a slight tendency to keep at about the same latitude. How far this might be due to observational bias, we are given no means of estimating. But the experiments were not on a very large scale, in all 42 birds being released and 29 recovered. The western releases, when examined closely, do not appear to show any significant directional tendency. Although the total flight vector given by Yeagley appears significant, this is apparently spurious, being due to the inclusion of the two Waterman (Illinois) birds which happened to have flown west, but which were actually released well *within* the tangency line and should, therefore, have been included in the second group. In the eastern releases there appears, at first sight, to be a significant tendency to return to State College, but on further examination the meaning of this seems very doubtful. These birds had been trained up to 70 miles round State College and of the 5 birds which reached home only 2 were released further than 70 miles distant, and 1 bird of these 2 took 10 days in which to accomplish the journey. Finally, there is the reverse experiment, described as the 'Cozad Expt', in which birds trained at Cozad in Nebraska were released at Berkeley Springs, Pennsylvania: 12 birds were released and 6 recovered. The scale of the experiment is too small to justify much weight being placed upon it, but there is perhaps a slight tendency to home to the correct latitude. Whether this is significant or not, the data do not enable us to decide. To sum up : though the experiments as a whole were on a very large scale, they do not appear to give any satisfactory evidence for sensitivity either to magnetic or Coriolis fields.

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SOME PHYSICAL PRINCIPLES OF BIRD ORIENTATION

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The object of this paper is largely to present a destructive criticism of some recent suggestions as to the physical mechanism by which birds orient themselves on homing (and migratory) flights. In particular the hypotheses due to Ising (1) and Yeagley (2) will receive attention. The first author suggests that a bird may determine its latitude and direction of flight relative to a great circle of longitude by the use of Coriolis forces—a rough account of whose nature is presented later. The second author also uses the Coriolis-force hypothesis for latitude determination, but suggests in addition that a second co-ordinate, not longitude, but something effectively equivalent to it, may be provided by the vertical component of the earth's magnetic field.

The Coriolis-force hypothesis for latitude determination is new, but the magnetic field idea has recurred in various forms for a very long time. Although there is no objection in principle to their application, it will be shown that the

chances of a bird being able to utilize them in practice are extremely minute and that both may be dismissed from reasonable consideration.

Before embarking on a discussion, however, it is well to distinguish between the problems of homing and migration from the point of view of the quality of the information which the bird must possess. In migration it is very much a question of flying a known beat, that is, progressing in one general direction knowing that such flight will ultimately bring one into familiar regions. In homing the direction which this flight must take is not known. The essential difference is that in migratory flights the bird knows where it has started from, so must merely steer a true course and wait for home to appear. A homing bird does not know where it has started from so its problem is of a different order. That some migratory birds tend to fly in a given direction rather than to a given place is well shown by Rüppell's experiments (3). Being the more complete problem, homing will be discussed in this paper.

Now home must obviously be characterized by a co-ordinate system having two variables. If the world were flat, the natural choice for these would be the x and y of an ordinary piece of graph paper. The world is round, and we ourselves find a natural choice of co-ordinate system in latitude and longitude. It is suggested by Yeagley (2) that the bird's choice is latitude and the lines of constant vertical intensity of the earth's magnetic field. As the north magnetic pole does not coincide with the north geographic pole, the lines of equal vertical magnetic intensity are not lines of latitude, but are a set of rough circles cutting the circles of latitude. The fact that the sets of circles cut enables them to constitute the desired co-ordinate system. Since each pair of circles, one of equal vertical magnetic intensity, and one of latitude, cut at two points in general, home is ambiguous, there being generally the two points having the same characteristics of latitude and magnetic intensity. Yeagley calls these 'conjugate points'. Usually the ambiguity is not troublesome to the bird as the conjugate points lie far apart.

So when the bird is released, it must not only be able to measure the characteristics of the point at which it finds itself, but also be able to remember those of its home in order to know where to go. Now home is not effectively a point for a bird, but a fairly considerable area which it knows intimately. Thus very great accuracy in the determination and remembering of the characteristics does not seem necessary. As an example, we will consider a bird which desires to home with an accuracy of 25 miles at latitude 45°. The characteristics must then be measured to within about 0·5 per cent. This figure will be used throughout this discussion.

The magnetic effects will be considered first. If the bird were directly sensitive to a magnetic field, we have seen that measurement of it to 0·5 per cent., the field itself being about 0·5 gauss, is needed. There is no way in which a bird can be imagined to respond directly to the magnetic field in any sensitive manner though certain forces do certainly come into play when ordinary 'non-magnetic' matter is placed in a field. They are even tinier than those discussed later in connection with the Coriolis forces. Thus direct appreciation of the field may be ruled out. One's confidence in doing this is increased by the remark that when one subjects a pigeon to a field of about 1000 gauss, it responds in no way at all. If it contained an organ sensitive enough to detect a change of less than 0·005 gauss, surely the shock of a sudden application of 200,000 times such a field would cause some visible reaction on the part of the bird.

One turns then to other ways by which a bird may measure a magnetic field. It was suggested by Yeagley that the well-known laws of electromagnetic induction may help. His explicit suggestion was in terms of the linear translation through the magnetic field of some conductor. If we take a conductor of length 1 cm. and move it at right angles to its length with a velocity v cm./sec. through a magnetic field H gauss which is at right angles to the plane swept out

by the conductor, a potential difference of magnitude Hv/c absolute electrostatic units is induced between the ends, c being the velocity of light. In concrete terms, if a bird contains such a conductor (say a salty solution though the exact degree of conductivity is unimportant) and flies at 40 m.p.h., a potential difference of about 10^{-5} ordinary volts is induced. This the bird must measure to better than 10^{-7} volts in order to achieve the desired accuracy. Now it must be remarked that this potential difference cannot create a current. All that happens as the bird accelerates from rest to 40 m.p.h. is that a separation of charge takes place until the force on a given electron due to its translation through the magnetic field is balanced by the electrostatic forces due to the non-uniform charge distribution. Thus the bird must make a purely electrostatic measurement to within 10^{-7} volts. It may be remarked that the most common electrostatic instrument in a physics laboratory—the cathode-ray oscilloscope—can just about detect 1/10 volt. However, the minuteness of the effect is not our only objection to its utilization. Firstly, the bird must know its speed to better than 0·5 per cent. Secondly, one must consider the earth's electrostatic field. This ever-present field has a magnitude of about 1 volt per cm.—10^5 times bigger than the effect being measured. Thus the bird's problem would not be the measurement to 10^{-7} volts in 10^{-5} volts, but in 1 volt—an accuracy of 1 part in 10^7 rather than 1 in 100. This assumes that the effect of the earth's electrostatic field is anything but constant and may change by some per cent. in a short distance. In addition, there are the effects of atmospheric electricity in the shape of charged clouds to be reckoned with. In other words, the bird would have no idea how big was the background field to be subtracted from the total effect, let alone estimate the difference to 10^{-7} of the total. We may, therefore, conclude that the induction effect as conceived by Yeagley is not operative.

There is, however, a second way in which electromagnetic induction may be used to measure the magnetic field. This gets over the difficulties due to the necessity of knowing v and the earth's electrostatic field, and the fact that the measurement must be an electrostatic one, and should be considered before discountenancing completely the magnetic hypothesis. If, instead of a straight conductor which is uniformly translated through the magnetic field, the bird's anatomy contains a conducting loop which is oscillated in the field, an alternating current is induced in the loop. This is simply the dynamo principle. The bird is no longer called upon to make an electrostatic measurement, but has a current to measure. v need no longer be known, but only the frequency of oscillation ν, a much simpler matter. Most important, the effects of the earth's electrostatic field, very much bigger than the desired effects in the first method, may be much smaller now—by a factor of roughly $10^5/R$, R being the resistance in ohms of the loop. It therefore seems that here is a satisfactory way of measuring the field H. The stumbling-block is again the magnitude of the effect. The current induced is of order $\nu H/R\ 10^{-8}$ ordinary amps. for a loop of area 1 cm.^{2} ν cannot be much bigger than unity. Assuming R to be as low as 1 ohm—a very generous figure—the current is then about 10^{-8} amps., which must be measured to better than 10^{-10} amps. In assessing the bird's chances of being able to make such a measurement, one must bear in mind the much bigger currents of physiological origin present in living matter.

It therefore seems extremely improbable that birds are able to make the desired measurement of the earth's magnetic field.

We now consider the determination of latitude by the use of the Coriolis forces. First of all a short account of the nature of these forces. It has often been implied that they are essentially connected with the rotation of the earth, but this is quite untrue. Consider the case of a particle of mass m situated on a disc which revolves with angular velocity w (frequency $w/2\pi$). If it is situated at a distance r from the axis, its sideways velocity is rw. If it now moves

inwards a little radially on the disc which continues to rotate, r will get smaller, so the sideways velocity will fall below rw. But now, if the sideways velocity has diminished, there must have been some sideways force experienced to produce the diminution. This is the Coriolis force, and if the radial velocity is v' it has a magnitude $2mwv'$. The Coriolis force is thus a purely geometrical effect produced by movement along a certain curve—the disc is just a convenient fiction of course, the same forces being experienced if the particle moves along the same course in space as we have imagined it to follow on the surface of the disc. If now the bird is either at rest on the ground or flying a perfect course, its instantaneous rotation will indeed be that of the earth, and we may speak of the Coriolis force due to the rotation of the earth. If, however, it flies a course which is a part of a circle at such a speed that its instantaneous angular velocity becomes comparable with that of the earth, the spurious Coriolis forces due to this inaccuracy of flight become comparable with those due to the rotation of the earth and so the desired effects are masked. Before then we begin to consider seriously the Coriolis-force hypothesis for a flying bird, we must decide whether it is possible to fly a true enough course to permit of an unambiguous interpretation of the Coriolis effects. If we take as criterion that the bird's flight should have an angular velocity less than that of the earth, this amounts to a demand that our 40-m.p.h. bird should fly a course whose instantaneous radius of curvature should be greater than about 100 miles. Putting it another way, the course must be true to better than 1/50 in. in 100 ft. This is manifestly impossible as the up-and-down motion even between alternate wing beats must be greater than 1/50 in. Though we have seen already that the use of Coriolis forces by a flying bird is impossible, we will proceed with the investigation to show how, even ignoring this objection, the bird's task is an impossible one.

The Coriolis force may in principle be used to determine latitude since, at latitude λ, a bird flying due north is effectively flying towards the earth's axis with a velocity $v \sin \lambda = v'$. The Coriolis force, therefore, varies as $\sin \lambda$.

There are two chief ways in which the Coriolis force may be used. They bear considerable resemblance functionally to the methods of electromagnetic induction discussed above. The first and again cruder method is that suggested by Yeagley (2) being the analogue of the straightforward translation of the conductor in the magnetic case. Yeagley simply considers the expression $2mwv \sin \lambda$, the sideways force acting on a bird of mass m flying with velocity v at latitude λ, and says that, if the bird knows its velocity v (to about 0·5 per cent. again), it can find λ by measuring this force. Inserting numerical values, we find that the Coriolis force at $\lambda = 45°$ is about 1/6000 of that due to gravity. Now there is no difference at all in the effect on the bird of the downwards force of gravity, and the sideways force 1/6000 as great, of the Coriolis type. Thus, the only effect on the bird is that gravity now seems to act at a small angle (less than 1 min.) to its true direction. This angle must be measured to 0·5 per cent., so must be measured to within a few tenths of 1 in. sec. of arc. This in itself would seem an impossible task, but is rendered more so by the remark that the bird has no idea where to measure this small angle from. Gravity itself cannot be used since that is already being used to supply the direction of the resultant force. Unfortunately, gravity does not act at right angles to the surface of the earth because of its centrifugal component, the effect of neighbouring elevated masses, the local configuration of the countryside, and so on. One must also consider the buffeting by the wind to which the bird is subject. This is always changing and much in excess of 1/6000 of its weight. Yet another objection to this naive view of the situation, is again concerned with the truth of the flight. Unless this is impossibly high (the same order as remarked above), the plain centrifugal force will exceed the Coriolis and, of course, be indistinguishable in its effects. Thus not only must the bird be able to fly such a true course, but it must know

that it is so flying so as to be able unambiguously to interpret the effects as Coriolis rather than centrifugal in origin. This demands clear and distant sight of a fixed object on the ground. Such Ossa upon Pelion disposes definitely of a simple perception of Coriolis force for latitude determination.

There remains, however, the second suggestion for the use of Coriolis forces due to Ising (1) which came first chronologically. This is the analogue of the rotating-ring method in the magnetic induction case and, as there, removes some of the major objections—the necessity for knowing v accurately and the disturbing effects of gravity. Though the overriding objection as to truth of flight remains for a flying bird, this method may be used by a sitting bird so must be further investigated. Consider a ring-shaped vessel containing a fluid. This ring is imagined to be horizontal and rotates about a diameter at right angles to the axis of the earth. The fluid to the north of the diameter now moves towards the axis of the earth, let us say, and so experiences a Coriolis force in one direction. The fluid at the other side of the ring moves away from the axis of the earth, so experiences a Coriolis force in the opposite direction. These oppositely directed forces produce a swirling motion of the fluid round the ring whose magnitude is again simply related to the latitude. Ising suggests that the bird perceives this swirling motion, determining its latitude thereby. Again, one's objection must be based on the magnitude of the effect. A discussion has been given previously (4), where it was concluded that the energy available was far too small to give a reasonable chance of detection, let alone measurement to within 0·5 per cent. A ring of 1 cm. diameter and 1 mm.^{2} cross-section rotated through about 6°, generates energy about 10 times greater than the Brownian agitation energy of a single degree of freedom of whatever device is used to detect the energy. This energy is contained in the fluid filling the ring and only a small fraction could be transferred to the detecting device. The energy generated depends very strongly on the scale of the ring—a reduction by a factor of two producing roughly a hundredfold loss in the energy generated. Though various organs such as the eye and ear are extraordinarily sensitive, the energy input for mere detection of the stimulus is always considerably in excess of the Brownian energy. Here measurement to better than 1 per cent. is demanded when the stimulus is of the order of the Brownian energy, or perhaps considerably less. Many devices may be considered which would increase the relative sensitivity of the detector to the Coriolis energy, but it seems most unlikely that adequate sensitivity could be attained. One should also bear in mind that energy will be transmitted to the fluid purely by inertial and elastic effects when the ring is rotated and also that swirling motion of the fluid would be induced by a rotation of the ring about its centre—the usual use of the semi-circular canals suggested by Ising as the fluid-containing ring.

It therefore appears that the use of Coriolis forces for latitude determination is as improbable as the use of the magnetic field. It should be emphasized, however, that the above analysis has not shown the observations to be impossible in principle, but merely that they seem most implausible to a physicist. It is for the biologist to have the last word—or perhaps for the bird.

Finally, I would like to draw attention to an aspect of homing which may have some importance. The natural explanation of homing is in terms of straightforward search by the bird—perhaps random, perhaps based on some plan such as a spiral. In either case this must be ruled out on the basis of the labour and time involved. Successful homing from long distances is accomplished in times much shorter than can be accounted for on the pure search hypothesis. Following this observation it is again natural to seek for some explanation of homing which enables the bird to proceed directly home—the homing in two co-ordinates, discussed above. If, however, the bird can home not in two co-ordinates, but in one only, say in latitude, the search labour in which it is involved to find home is greatly reduced. If a bird, instead flying straight home, flies to its

home latitude then turns and flies home, it will only have flown, at the most, about half as far again. Its chance of getting home is then 50 per cent. If it turns the wrong way, it may get tired of search after a certain time, turn, and reach home the other way. And surely latitude homing may be achieved with the aid of the sun, determination of whose highest point to within one diameter gives homing of the desired precision. Actual observation of the sun at noon is not necessary, occasional glimpses would combine with a time sense to enable its course to be constructed.

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POLISH INVESTIGATIONS ON HOMING IN BIRDS AND THEIR ORIENTATION IN SPACE

By ROMAN J. WOJTUSIAK.

The paper which I am about to read supplements to a certain extent a lecture delivered several years ago in England by Professor Kazimierz Wodzicki who was received here with great hospitality during the war. At that time British ornithologists showed much kindness to their Polish colleagues and adopted the Polish Section of the International Committee for Bird Protection, making it possible thereby for Polish research to continue in this department without interruption. This was important, inasmuch as at the same time the German occupants in Poland allowed the Poles to carry on no scientific work whatever. We wish to express here our deep gratitude for the friendly attitude adopted towards our colleagues who emigrated to England during the war.

The subject which I am to discuss deals with the problem of orientation in space in birds, in connection with homing and migration, on the grounds of investigations which we had the opportunity of carrying out in Poland from 1933 up to the present. The problem is an old one, but it continues to be of interest.

Although quite a number of papers dealing with the subject may be found in literature, the problem has not yet been adequately cleared up, and it has only led to the creation of a number of various hypotheses. The solution of the problem is of interest not only to biologists, being also of importance to nature protection. Flying in our geographical latitudes twice a year over distances which are frequently enormous, great masses of birds are exposed to various dangers causing great losses in their numbers. Man and external conditions play here the leading rôle. Knowledge of the influence exerted by the latter upon the course of migrations and orientation in space would allow us to understand the optimum conditions for flights and the effects experienced by migratory birds in consequence of deviations from the optimum.

Until some 15 years ago, apart from observations on carrier-pigeons, there were very few papers on this subject. Among the more important ones worthy of mention there is a large publication of the American investigators Watson and Lashley (1915) who transported certain species of sea-gulls to various distances and found them to possess a well-developed homing ability, and the work by Loos (1907) who carried out similar experiments with swallows and starlings. Encouraged by the abundance of problems facing scientists on the subject of bird orientation in space, Professor K. Wodzicki and I decided in 1933 to initiate together suitable experiments in Cracow. Our first aim was to investigate the

homing ability and flight velocity of swallows, and to acquire a knowledge of the influence of various external factors upon their ability of orientation. Subsequently, we carried on these investigations for a number of years, also together with Mr. B. Ferens, Assistant in the Department of Animal Psychology and Ethology, Jagellonian University, Cracow.

The technique of the experiments was very simple. Swallows were captured in the countryside, near their nests, ringed with aluminium rings of the Polish Station for Investigation of Bird Migrations at the State Zoological Museum (Warsaw), and marked on their throats with coloured Indian ink. Then the birds were transported to various distances from their nests, and set free at stated hours. The birds, which had left eggs or young ones in the nests, flew back and the exact time of their return was recorded at the nests.

Swallows belong to birds which perform long migrations along a north-south line. In order to find out whether the meridional direction has any special influence on their ability of orientation, or whether their return is independent of the points of the compass, the birds were transported in all directions north, south, east and west, as well as in intermediate directions. It turned out (Wodzicki and Wojtusiak, 1934; Wojtusiak and Ferens, 1938; Wojtusiak and Ferens, 1945 *a*, *b*), that the swallows' return to their nests was altogether independent of the direction in which the birds were taken. They returned just as easily along a north-south line as they did from an east-west direction, or from intermediate directions. Neither were any differences observable between the velocity of birds returning along meridional lines and latitudinal ones. Swallows, therefore, return to their nests irrespective of geographic direction.

A separate series of experiments dealt with the problem of the influence exerted by mountains upon the homing ability and orientation of swallows. From Mydlniki, near Cracow, the birds were taken southwards by rail and released in various localities situated in the Carpathians or in the Tatra Mountains (a rocky chain of high mountains lying to the south of the Carpathian range proper). We found that mountains are no real barrier for homing birds (Wojtusiak, Wodzicki and Ferens, 1937). Swallows returned to their nests both from lower mountain districts and from the shores of Lake Morskie Oko, situated in the core of the Tatra Mountains at an altitude of 1,393 metres and surrounded from the south, west and east by rocky ridges reaching up to about 2,000 metres above sea-level. Set free, the birds flew home usually along river valleys, avoiding mountain ridges on their flights. Such behaviour is in accordance with normal flights across mountains during seasonal bird migrations, which also take place chiefly along valleys. Although mountains do not make homing impossible for swallows, they seem, however, to exercise a certain influence on bird orientation. The mean homing velocity in mountain experiments hardly exceeded half of that in lowland experiments carried out on approximately the same distances.

In order to find out whether atmospheric conditions have any influence on homing ability and bird orientation, experiments were carried out not only on fair sunny days, but also on rainy ones, during storms and in fog. Not one of these factors proved to have a decisive influence on the powers of orientation in swallows. The birds returned to their nests just as well when they encountered on the home journey falling rain or a thunder-storm. Naturally, it was impossible to determine how the birds behaved in the rain or storm areas. It was only possible to prove the fact of their homing in spite of these obstacles on their journeys. Such conditions could at most bring about a diminution of the mean homing velocity.

Of particular interest to us were experiments with swallow flights on foggy days. We ascertained that birds return to their nests in spite of quite thick fog. This fact was observed on a route of 10·5 km. between Mydlniki and Rudawa, as well as between Mydlniki and Dulowa on a distance of 23·5 km. (Wojtusiak,

Wodzicki and Ferens, 1937). At first we did not pay any special attention to this fact. Now, however, it must be pointed out as it constitutes one of the points which uphold our conception of orientation in birds.

A separate series of experiments dealt with the problem of the influence exerted by night-time on the ability of orientation in swallows. In 1936, barn-swallows (*Hirundo rustica* L.) were captured at Mydlniki and set free at night in the localities of Liszki, Rybna and Alwernia, at distances of 10, 16 and 22 km., respectively, to the west of their nesting sites. Night-time proved to be no real obstacle to their homing ability. The swallows returned, displaying only a mean homing velocity which was about one-half of that in day-time experiments. They also displayed certain differences in their mode of flying. In nocturnal experiments their flight had a fluttering character, and not a smooth gliding one as during day-time flying. Swallows set free at night returned to their nests at various hours of the following day, according to the distance. Particularly interesting and worthy of emphasizing is the fact that one of the swallows returned from a distance of 10 km. even before dawn, at 2·14 a.m., others at 3·23, 3·24 a.m., etc. This is evidence that birds find their way home even by night.

In many of our experiments there was noticeable a characteristic behaviour of the birds at the moment of their release. The swallows soared up into the air, described one circle or several, and then started to fly in a direct line towards their nesting site. Only in some cases was it impossible to determine the direction chosen by the birds at the starting-point, Occasionally, the swallows chose a direction along a railway-line not in accordance with the direction in which their nests lay. However, it must be pointed out that in most cases, immediately upon their being set free, there was observable a distinct orientation of the birds in the direction in which they ought to fly towards their native locality. Of a total of 28 experiments, we succeeded in 19 cases in proving a distinctly directional course of the birds' flight immediately upon their being set free, while only in 9 cases the initial start deviated from the proper direction. Such a directional course of the flight of homing swallows is deserving of particular attention. The first circles described by the birds serve to orientate them in their position, then they find the proper direction in which their nests lie.

At first the swallows were taken short distances, not exceeding 120 km. from their nests. In subsequent experiments we increased these distances. Already in the very first experiments (Wodzicki and Wojtusiak, 1934) of particular interest was the ascertained fact that birds released in localities situated nearer their nesting sites, returned at a slower rate than those homing from greater distances. The increase of the mean homing velocity for distances not exceeding 120 km. was directly proportional to the distance between the release point and the swallows' native locality. By the way of example, it will suffice to state that the mean homing velocity calculated for swallows transported to a distance of about 120 km. amounted to almost 35·5 km./h., and was about 7 times greater than that for birds taken to a distance of 10 km., the mean homing velocity in the latter case amounting to 5·7 km./h.

It was obvious that the homing velocity of swallows could not increase indefinitely along with the distance, because this would lead to fantastic speeds. In order to find the limit of distance up to which that odd increase of velocity still takes place, we transported the swallows in subsequent experiments to greater and greater distances, up to 660 km. It turned out that the homing velocity increases only for distances not exceeding 120 km. For greater distances it is maintained on approximately one level, about 10–15 km./h.

In order to secure better grounds for a more general consideration of the subject, we took into account the investigations of other authors carried out on swallows, especially those of Loos (1907) and Rüppell. The latter investigator initiated his experiments on orientation powers in birds almost simultaneously

with ours. Our aim was to analyse in greater detail the separate factors exerting an influence upon bird orientation, and we therefore made efforts to transport as many birds as possible to designated distances, whereas the above-mentioned author tried to investigate the homing powers from various distances. It turned out thereby that homing takes place even when a swallow is taken to a distance of 1,850 km. from its nesting site (Berlin–Madrid). Furthermore, the latter distance is not necessarily the ultimate homing limit.

When properly recomputed, the results obtained in the experiments of Loos and Rüppell proved to be a conformable supplement of our own. The homing velocity for distances exceeding 120 km. showed no increase, maintaining a uniform level.

Of particular interest to us was the distance of about 120 km., beginning from which the mean homing velocity of swallows ceases to increase. A study of the records shows that from a distance of about 120 to 150 km., swallows return to their nests within one day. For greater distances the birds need more than 24 hours to accomplish their homing journey.

We tried to explain the facts observed by us by assuming the existence of a twofold mode of spatial orientation in swallows. When the distance from their nests does not exceed some 120 km., the birds can get their bearings in the vicinity from optical details remembered from their daily flights. An area with a radius of 120 km., *i. e.* within range of the swallows' one-day flights, would be familiar territory to the birds. The increase of homing velocity along with the increase of distance within such an area is explicable with the aid of the hypothesis that birds are actuated here by a psychical factor : self-confidence in territory which is familiar, and a state of incertitude in strange territory (Wojtusiak, 1934). A bird which finds itself at a small distance from its nest is familiar with the terrain and is not alarmed by the fact that it must find its way back to its nesting site. The greater the distance the stranger becomes the locality and the greater is the bird's alarm, which impels it to a fast homing flight. Along with the increase of distance, another type of spatial orientation comes more and more to the foreground ; this new type of orientation is made possible by the existence of a hitherto unknown sense which may be termed a ' sense of direction ' or ' sense of orientation '.

At distances which exceed some 120 km., *i. e.* in territory which is unfamiliar to birds from their daily flights, swallows lack orientation on a basis of optical details remembered from their everyday flights. Homing takes place exclusively in consequence of the activity of the ' sense of orientation ' or ' sense of direction '.

The preceding picture is seemingly complicated by the fact that for distances of about 120 km. the mean homing velocity exceeds 35 km./h., while for distances above 120 km. it stays approximately on a level of about 10–15 km./h., being, therefore, more than two or three times smaller. This apparent decrease of the homing velocity for distances exceeding 120 km. is easily understood if we take into account the fact that our first computations of homing velocity were carried out as if the birds were in flight during the whole time, without resting. However, we have seen that swallows need more than 24 hours to return from such distances. Apart from the flying time itself, we must also take into account the time necessary for sleep and for rests during day-time, as well as for finding food, for encounters with other birds, etc. Upon deducting the night hours, the mean homing velocity rises, although it does not reach the maximum velocity determined for a distance of 120 km. (Wojtusiak and Ferens, 1938). It reaches that maximum when we also add the time necessary for resting in day-time, for hunting food, etc. The flying-time itself at which we then arrive amounts to 4–8 hours per day, this being in accordance with the suppositions of some authors who, as for instance Floericke (1928), assume that the actual flying-time for most birds amounts

to 4–8 hours per day, while for the stork it rarely exceeds 4 hours. Therefore, a swallow returning to its nest from a point lying outside the range of its everyday flights has a constant daily velocity, which is approximately the maximum velocity it can develop. Inasmuch as the number of daily periods necessary to return home increase along with the increasing distance, while the homing impulse remains unchanged, the above-mentioned velocity is maintained on a uniform level for all distances above 120 km.

The above-quoted facts referring to the homing velocity of swallows returning from various distances stand in sharp contrast to the results hitherto obtained in experiments with *carrier-pigeons*. According to Professor E. Rabaud (1927) the latter birds taken to various distances from their nests, return at a higher speed from smaller distances than they do from greater ones. Observable in carrier-pigeons was a distinct dependence of orientation powers upon training. The above-mentioned author considers pigeons to be guided on their home journeys by optical details registered in their memory during previous flights ; therefore he considers them to be guided by memorized orientation. Griffin, and after him Gray (1946), assume that a bird taken outside the limits of the territory with which it is familiar from everyday flights, finds its nesting site by exploring an enormous area by flying in a spiral line, the beginning of the centrifugal spiral being the point at which the bird is released. Therefore, the greater the distance from which the pigeon is to return, the smaller is the bird's mean homing velocity. With swallows we can in no case demonstrate a decrease of homing velocity proportional to distance. Swallows fly straight for their nests without any spiral exploration. For this reason we are obliged to assume that swallows possess a directional type of orientation, which we shall discuss in detail later on. A memorized type of orientation occurs in swallows only in territory familiar to them from their everyday flights, therefore, to a distance which does not exceed 120 km. from their nests. However, here also we have a well-marked difference as compared to carrier-pigeons, the fact being as already mentioned, that for short distances (near nests) the homing velocity is comparatively small, while an increasing distance brings about an increase of the homing velocity. We endeavour to explain this fact by the smaller or greater anxiety felt by birds in localities with which they are more or less familiar.

For the purpose of ascertaining whether all birds possess homing powers in an equal degree, or whether migratory birds above all are distinguished by this feature, we carried out experiments with sparrows in 1939 and 1947 (Wojtusiak, R. J., Wojtusiak, H. and Ferens, B., 1935). These birds lead a more or less settled mode of life, or at least they do not go on distant seasonal migrations. Sparrows caught in the Botanical Garden of the Jagellonian University in Cracow were taken to various distances from their nests, ranging from 2·7 to 33 km. The results so far obtained demonstrate that these birds return to their nests only from distances not exceeding 11 km. Of the birds taken to greater distances no return has been yet recorded. These experiments seem to indicate that the ability of homing from great distances is above all a distinguishing feature of migratory birds, but not so of settled ones.

Our acceptance of a twofold manner of spatial orientation in swallows compelled us in consequence to occupy ourselves more closely with an analysis of both types of orientation by experimental investigation.

In 1939 we devoted separate experiments to the rôle played in the orientation of swallows by memory and by the ability to learn optical route details (Wojtusiak and Ferens, 1945). Our aim in these experiments was to ascertain whether a change of homing velocity takes place in birds transported to the same locality for a second time. Such experiments, carried out with four swallows, brought quite clear results. Only one swallow, released at Kielce at a distance of 105 km., displayed on its second flight a slightly smaller homing velocity than on the

first one. The second bird, employed twice on the route Kielce–Mydlniki, displayed on its second flight an almost twofold increase of velocity. The third bird, released at Radom (172 km.), showed an increase of velocity which was more than quadruple, while the bird employed on the route Warsaw–Mydlniki (254 km.) returned on its second flight more than four times as fast as it did on

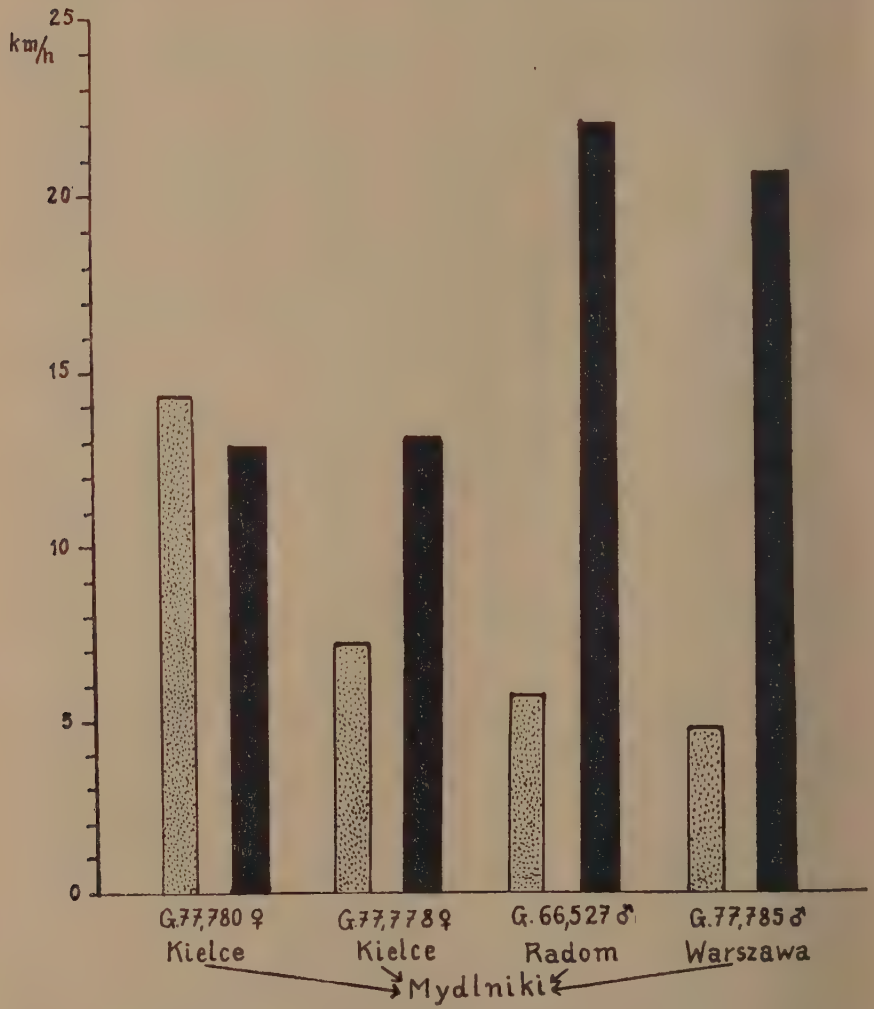

Fig. 1.—The influence of memory upon the orientation in space in Swallows (*Hirundo rustica* L.). Dotted diagrams—The velocity of the first return. Dark diagrams—The velocity of the second return.

its first journey. Swallows, therefore, display a distinct ability for learning the route of their flight, and visual memory may play an important rôle in their spatial orientation within distances which they can cover in one-day flights.

As regards the problem of the other type of orientation in space, and the essence of the unknown ' sense of orientation ' or ' sense of direction ', Professor

Wodzicki and the author came forward with somewhat different conceptions. Professor Wodzicki drew attention to the possible influence of terrestrial magnetism on directional orientation in birds. Birds could be guided by magnetic lines in the manner of a compass, the magnetic sense being located in the internal ear, in accordance with the opinion of Stresemann (1935) who assumes that birds react to terrestrial magnetism with the aid of otoliths. Consequently, having been given a chair in the Superior School of Rural Economy in Warsaw, Professor Wodzicki initiated suitable investigations on storks. Experiments carried out in 1937 by Professor Wodzicki, together with his associates, ascertained the fact that storks possess an excellently developed sense of orientation in space. Storks were captured at Butyny, in the Lwów province, and at Moroczyn, in the Lublin province, and sent to distances of 50 km., 111 km., 306 km. (Warsaw), 660 km. (Bucharest), and 2260 km. (Lydda in Palestine). The birds returned from all the points, irrespective of their geographical position. In 1938, similar experiments were carried out on the route Butyny–Lisbon (2700 km.), Butyny–Berlin (680 km.), and Butyny–Harviala (Finland, 1132 km.). In each series of experiments four birds were employed. In order to investigate the possible influence of terrestrial magnetism on orientation in birds, some of the birds in each series had magnets attached to their heads. The magnetic fields of these magnets were stronger than the terrestrial magnetic field. The remaining control-birds had attached to their heads ordinary iron bars, instead of magnets. Of all these birds only three returned, from Berlin; two of them without magnets, and one with a magnet. Their homing velocity was somewhat smaller than that of the birds in 1937. These experiments did not give a complete solution to the problem, on account of the inadequate number of birds. However, they seem to indicate that exclusion of the influence of the terrestrial magnetic field on birds does not have any effect upon the homing powers, as such, of storks. Here, also, one could observe that, immediately upon being released and soaring up into the air, the birds chose at once the proper homing direction, or one close to it.

On the other hand, I from the outset, directed my attention rather to electromagnetic radiation. The first basis, therefore, was suggested by a fact, quoted by E. Rabaud (1927), saying that according to certain authors disturbances in the orientation powers of carrier-pigeons occur when these birds find themselves in the vicinity of a short-wave wireless station which is broadcasting at the moment, and also during storms (Knieriem, 1942). In experiments with swallows, we ourselves had no opportunity of confirming the latter fact. Our starting-point was the indisputable directional character of the flight of birds released in a strange locality. The birds soared up into the air and having usually described but a few circles above the release point, they would choose the direction in which lay their nests. Such orientation took place both in day-time and at night, and equally well on a fair day, as in a fog. Such powers resemble radar, employed in World War II. The birds seem to 'grope' around, with the purpose of finding the proper direction. Having found it, they fly straight towards their native locality. The radar method of orientation in space is known to exist in bats in which, however, it is based on the principle of sound-waves which are outside the range of ordinary perception (Vesey-Fitzgerald, 1947). A bat emits from its mouth high tones and perceives them with the aid of suitable sensory organs. Sound-waves, reflected from neighbouring objects, inform the animal as to its position in relation to surroundings. In birds, having orientation in day-light, at night and in fog, one should rather assume that the active factor here is electromagnetic radiation, invisible indeed to human sight, but passing through fog and existing also in darkness. We encounter radiation of this type as radio waves and infra-red waves.

The assumption of a radar-like method of orientation in space is very attractive ; it introduces, however, two unknown factors into the problem : the question of emitting and perceiving radiation of a given wave-length. In order to simplify the problem, we decided to confine ourselves to the analysis of only one unknown factor, the second one, *i. e.* to the question of whether birds can really perceive, as a sensation, long-wave electromagnetic radiation which is invisible to human beings. Advancing into the foreground were infra-red rays, being as they are closely associated with red rays which are visible to human beings and to birds.

I expressed my views in the form of an appropriate hypothesis (Wojtusiak, 1946). A basis for accepting the existence in birds of hypothetical powers of perceiving infra-red rays, and of the influence of such powers on bird orientation, was discovered by us in experiments on the colour sense in birds and tortoises. Both groups of animals possess in their optic retinas characteristic corpuscles of fat, coloured orange or red. These corpuscles have the effect of a colour filter, letting through long-wave radiation and reducing that of short waves (Henning, 1920, Wojtusiak, 1933). This fact allowed Henning to assert that tortoises as well as birds, owing to their increased sensitivity to red and orange colours, are able to see through fog, this fact making orientation in space easier for them. Honigmann (1921) criticized this view, pointing out with good reason that if the ability to see red and orange colours were to assist these animals in seeing through fog, then human beings would not fail to take advantage of this fact. A ship-captain or aeroplane-pilot, putting on the right kind of spectacles, would be able to navigate in fog. Personally, I was of the opinion (Wojtusiak, 1937), that the whole matter had not been properly cleared up in the discussion conducted by the above-mentioned authors. Birds and tortoises could possess orientation in fog if they had the power of perceiving infra-red rays, invisible to the human eye. The probability of the latter fact seemed to us to be very great, and in this direction we undertook investigations on the two groups of animals, birds and tortoises, possessing fat corpuscles permeable to long-wave radiation.

The advantages of accepting the hypothesis of infra-red perception were quite considerable, both as regards birds and tortoises, as well as in relation to a number of other animals, vertebrates and invertebrates, which lead a nocturnal mode of life. First of all in regard to birds, we should be able to gain an understanding of the directional character of their migrations. During their autumn migrations birds fly towards warmer regions which, containing a considerable amount of infra-red radiation, would appear to birds as being brighter than the cold northern regions. In spring the reverse would take place. Owing to this, flights on a north-south line would be explicable by optic sensitivity, without need of having recourse to a hypothetical ' sense of orientation', ' sense of direction ', etc., and particularly a magnetic sense. The known fact that migratory birds when flying keep to river courses and coastlines could be explained by the sharp boundary between zones of a different intensity of heat radiation, *i. e.* between land and water. Seeing infra-red rays would make it possible for birds to see through fog, and it would explain the fact of swallows homing in our experiments conducted on foggy days. At the same time their range of vision would encompass a much larger territory than is possible for human beings. Infra-red radiation being emitted also in the night by heated objects, birds would be able to see not only in day-time, but also in darkness. This would explain the homing of swallows in our nocturnal experiments. According to Rabaud (1927), carrier-pigeons can also return home at night. Furthermore, this would also explain the fact that during seasonal migrations many species of birds which normally lead a diurnal mode of life, for instance most song-birds, fly by night. Moreover, birds prefer dark and sultry nights, not fair and moonlit ones. Thereby eliminated is the influence of lighting by visible radiation, while

what remains is almost exclusively heat radiation, which appears bright to animals and constitutes their indicator of direction. The ability to see infra-red rays could also clear up the hitherto unexplained arrival of great numbers of flower-loving birds, for instance humming-birds, in a vicinity in which on that day, or especially that particular night, a certain plant species, pollinated by those birds, bursts into bloom. At other times such birds are rare in the local fauna. This could be caused by the fact that such flowers can emit infra-red rays and so become visible from afar, especially at night. It is a known fact that in some plant species the temperature of the flowers is higher than that of the surroundings (Szafer, 1927).

The hypothesis that animals, and especially the birds in which we are interested, are able to see infra-red rays, would remain as but one more theoretical speculation if it were not supported by suitable investigations. We, therefore, decided to find out experimentally whether infra-red rays are actually visible to the animals to which Henning attributed powers of seeing in fog, *i. e.* tortoises and birds. We began simultaneously investigations on both groups of animals, belonging to different classes, since they are united by a common characteristic : the presence of red and orange-coloured fat corpuscles in their eyes. Furthermore, water tortoises are easier to experiment with than birds, and it could therefore be expected that they would sooner yield decisive results. Our suppositions were indeed completely substantiated. By applying a method of training we succeeded in ascertaining that tortoises are able to perceive infra-red radiation, invisible to human beings. The fact is that they distinguish between two lighted sectors having an equal amount of radiation and an identical colour to human eyes, but differing from each other in the quantity of infra-red rays which they contain (Wojtusiak, 1947). Particularly instructive are the hitherto unpublished results obtained in the latest experiments with a filter permeable exclusively to heat radiation. Two beams of light from a Vitalux lamp, which emits infra-red rays of a wave-length up to 4,000 mμ, were projected upon a screen in a dark room ; one beam was passed through the above-mentioned filter, while the other through a red filter and a two-centimetre layer of a 2·5 per cent. solution of cupric chloride ($CuCl_2$), absorbing infra-red rays. The animals chose on the screen the sector, indistinguishable to the human eye through its brightness or colour, on which were projected the infra-red rays, avoiding, on the other hand, the red sector which is plainly visible to the human eye.

Similar experiments on birds are in progress, and they already promise equally positive results. Pigeons were trained into the habit of taking food under the light of the Vitalux lamp, with a full content of infra-red rays. When offered a choice of two dishes, one of which was illuminated with the white light with a full content of infra-red rays, while the other was illuminated with white light deprived of a considerable portion of heat radiation up to 1,500 mμ wave-length, the birds in most cases chose the ' training ' dish, in spite of the fact that the position of the dishes was continually changed in order to avoid the possibility of the birds becoming accustomed to the position of the dishes in space. The results of these experiments are, therefore, similar to those with tortoises, and they seem to indicate that birds are able to see infra-red rays.

Further investigations ought to be conducted in the same direction, and they are already in progress. They may contribute to the clearing-up of at least a small part of the problem concerning spatial orientation in birds.

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DISCUSSION

Dr. A. LANDSBOROUGH THOMSON. I have listened with great interest to the opening speeches, and also with a certain amount of dismay as I found all the points I might make were covered. I feel that all I can do is to pick out and emphasize some of the points that seem to me to be most striking from the angle of a student of bird migration.

In the first place, we have to admit that our ignorance on this question of bird navigation is so great that we cannot afford to neglect any suggestions however far-fetched they may seem.

The second point is that migration is a wider problem than homing. Very likely, up to a point the navigation problem is the same ; but there is much

more in migration than in homing. The first is finding an unknown goal, the second a known one ; but if we could understand homing, we should be a long way towards understanding the navigational basis of migration.

As regards the suggestion that young birds migrating for the first time without their parents might have a tendency to go southwards, towards the Equator, one must remember that much migration is not in the north–south line, particularly in this part of the world. We have a great deal of migration taking place due east and west, and very commonly on a north-east–south-west line. We have also to consider trans-equatorial migration, where the bird is going right across the Equator to a southern latitude.

The third point I wish to emphasize is that, although visual recognition does not give us the complete answer, so far as we can tell, it does give us a lot of the answer ; we must not relegate it to a back seat because it does not seem to explain everything. I do not think there is any doubt at all that visual recognition plays a very large part in the orientation of migrating birds.

I do not want to go into all the evidence, but I recall one very vivid impression of my own in the field, at the south-east corner of the Baltic, when I saw hooded crows and other birds migrating from Russia along the Baltic coast of Germany ; and just at the place where I was standing, the beach turned away at an angle, and the flocks, as they flew along the coast and came to the angle, shot out over the sea, but in quite a short while they seemed to realize that they were over the water, and they rectified their direction and came back to the line of the shore. They were obviously following that line. A lot of observations have been published on the way that birds flying over the land adjust themselves to some geographical feature. Some small birds do not like flying across even small stretches of water ; they tend to go round. They may also vary their altitude according to the nature of the ground ; they tend to go higher when flying over ground that would not give them good cover.

As regards flying at night, it seems to me that when one is thinking of coast lines, where you have the sharp contrast between sea and land, and to a lesser extent in the case of rivers, there are probably very few nights when there is no possibility of following a feature of that kind.

As regards Dr. Thorpe's question, I do not think I can give a precise answer as to whether small birds migrate by night more often over sea than over land. There is great variation between different species as regards flying at night, and there are also differences in different parts of the world. There are parts of Europe where you see much more diurnal migration than in this country.

Griffin, whose work has been mentioned, has suggested that one could go a little beyond visual recognition of particular topographical features, to recognition of general geographical characteristics, and that might even extend to characteristic cloud formations. You might get visual orientation of this kind to a known area, and then have your detailed recognition. It is quite an interesting suggestion, which extends the possibilities of visual recognition.

I am not saying that that explains all migration or all homing. The inadequacy of vision as a complete explanation has given attraction to various alternative theories, particularly to the idea of some magnetic sense. That was put forward many years ago in a simple form, that a bird could use terrestrial magnetism as if it had a compass in its head ; and then it was recognized that a compass is not enough. Quite a long time ago somebody in France produced a grid theory in which the co-ordinates were provided by horizontal and vertical components of terrestrial magnetism. Then we had the Coriolis theory quite recently ; and now Yeagley has produced a new grid in which one co-ordinate is magnetic and the other is Coriolis. That is roughly the history of these various theories.

Interest at the present time is rather centred on this recent paper of Yeagley's. I am unable to go into the physics of the matter, but I must say that, so far as I am capable of following the subject, I am in agreement with the other speakers. It seems to me that the theoretical basis is extraordinarily difficult to accept. It demands a capacity on the part of the bird to perceive two quite different kinds of force, an electromagnetic force and a gravitational force, and to have some power of interpreting these in combination. That seemed to me extraordinarily difficult even without hearing the exposition we have had to-day.

The other criticism is of the experimental evidence produced by Yeagley. I have not gone into it so fully as Dr. Thorpe and his colleagues, but it seems to me that taking the ' average flight vector ' of birds released from a point was quite a fallacious method of interpretation. With one or two exceptions, although these happened to be particularly long-distance birds, none of the birds actually did return to the loft itself.

Apart from the interpretation, the planning of the experiments seemed bad. The birds were taken to the ' conjugate point ' and accustomed to that point before being taken to the release point. They should surely have been taken to the release point first. In any case, the results do not seem fully capable of the interpretation placed upon them.

There was one experiment which was not repeated, that of putting magnets under the wings of one group of homing pigeons, and equivalent weights under the wings of a control group. The results were fairly striking ; there seemed to be a definite advantage on the part of the control birds over the birds carrying magnets. But that is quite out of line with such other work as has been done on the subject ; and I think all one can say about it is that one wants to see it repeated, as it is crucial.

One other point in connection with visual recognition : although it will not explain everything, I think visual recognition coupled with a capacity to maintain a constant direction would take one quite a long way. There is a possible alternative in the interesting suggestion, made this evening, of a possible power of homing to latitude.

Professor V. C. Wynne-Edwards. I have been very interested to hear this criticism of Yeagley's experiments. We should, I think, realize that Dr. Wilkinson was dealing with matters of physical fact. What we have listened to was the disproof of the magnetic theory, and of the possibility of using Coriolis force to explain the homing faculty. If one could think that we had heard the last of these theories, it would be an excellent thing.

I am delighted to learn that Griffin has now actually followed homing gannets by helicopter. Before the war I was present at one of his experimental releases of herring gulls. We watched it from the top of a 700 ft. hill in Southern Quebec ; the birds were released one by one at the foot of the hill and we watched them go off in a variety of different directions. They were visible for about five miles, and though they did not appear to have any idea where they were going, and did not apparently orientate themselves in that distance, the majority did ultimately return home to breeding colonies off the Massachusetts coast.

I have one small contribution to offer concerning the idea of ' latitude homing '. It is merely a suggestion which might be helpful. You can determine latitude and longitude by means of a timepiece only, without any other instrument. To do this requires observations of the time of sunrise and sunset. The day-length on any given date is sufficient to determine latitude, and the times of sunrise and sunset in relation to Greenwich time will indicate longitude. This method of latitude determination does not work, however, at the equinoxes. Birds and other animals have an excellent time-sense, and might readily detect differences in incidence of sunrise and sunset consequent upon travel towards the east or the

west. For every 100 miles they go to the east or to the west the difference is about 10 minutes. Knowing how precise birds are in their waking-time in the morning, you will appreciate what a difference of this order means.

I adhere to the view that in the end we shall find this whole phenomenon of orientation has a visual explanation. It cannot yet be fully explained on this basis, and instances which are impossible to explain are often brought up. In this connection I would like to refer to an apparently parallel instance in human navigation. During the war a well-known ornithologist, on his way to undertake official business in Washington, was not only able to keep his fellow passengers informed as to their approximate position day by day, although they followed a highly erratic secret route, but finally gave an expected time of arrival in New York which turned out to be remarkably accurate. This got to the ears of the Captain, who asked for an explanation. In fact the observer was exceptionally well informed as to the distribution and density of sea birds, such as fulmars and shearwaters, and coupled this with rough observations on the ship's course and approximate distance travelled. By this means he was able to make independent deductions regarding the ship's position in a manner incomprehensible to a trained navigator.

Mr. B. W. Tucker. I expressed the opinion before the meeting that at any rate as regards Yeagley's experiments, which for most of us have been the main centre of interest, there would be extremely little left for anybody else to say after Dr. Thorpe and Dr. Wilkinson had dealt with the matter. That expectation has been borne out.

It has always seemed to me an extremely remarkable reflection that in spite of the enormous advances that have been made in recent years in many biological fields, in the understanding of such things as the mechanism of heredity, the factors controlling development, and so on, we are still so very far from understanding the physical stimuli which are operative in bird migration and homing.

I had the opportunity of discussing Yeagley's results with Dr. Thorpe beforehand, so that I knew something about his analysis, and it seems quite clear that the alleged evidence is surprisingly uncritical and shaky in many ways. The physical data I am not qualified to discuss, but so far as I have been able to follow Dr. Wilkinson's exposition, it does seem to me to be completely convincing. I had felt before coming to this discussion that even though the biological evidence was very much open to criticism, at any rate a certain credit was due to Yeagley for having put forward what, at least in theory, did make a reasonable working hypothesis as to the nature of the physical stimuli involved and how they worked. But after what we have been told it looks as if Yeagley has gone rather badly ' off the rails ' in his own special field of physical data, as well as on the more biological aspect, and it seems to me we are very much where we started. We do not seem to be appreciably any nearer to a really satisfactory explanation of the phenomena, and in a way that is rather disappointing, but it does make one feel that it is extremely important to consider again just how much can be explained in terms of the ordinary senses. I would agree with Professor Wynne-Edwards that it seems probable that we can explain many migratory and homing phenomena in terms of visual responses, but they will not explain everything. I do feel very strongly myself, that the phenomena both of homing and migration are not completely explicable in terms of any of the straightforward known senses.

You can obviously explain a very great deal in terms of visual responses, and you can probably explain a good deal more than might appear at first sight. An organism may be aware of and be able to respond to less obvious variants

in the environment which one would not be inclined at first sight to take into account, but I would make this one general point. Although I completely agree with Dr. Landsborough Thomson that the factors and processes involved in migratory behaviour and in homing are not the same, it does seem to me that in searching for the physical basis of this kind of behaviour, one ought to look for stimuli of the same nature in the two cases. It seems to me very unlikely that the observed phenomena are to be accounted for in any way which does not give a convincing explanation of the whole field of behaviour in both those cases. If I were presented with a hypothesis of reaction to physical stimuli which appeared reasonable as applied to homing, but clearly broke down as regards migration, then I should feel very sceptical about the hypothesis. It seems to me probable that the basic physical stimuli involved are the same.

Obviously one should attempt to explain the observed behaviour in terms of known senses, and exhaust the possibilities before one turns to hypothetical and more or less imaginary senses. But it seems to me that any satisfactory explanation has got to account for such cases of migratory behaviour as 'hitting off' a little island in the middle of the ocean, and that of birds like penguins which are confined to the water, where one would have thought they had not available to them any possible visible stimuli which they could follow; yet they seem, after ranging far afield in the non-breeding season, to get back quite faithfully to the breeding ground, entirely by swimming. I suppose it is just possible that they might respond to differences in temperature, but it does seem to me a very difficult supposition, and I feel that any working hypothesis on the subject which is going to be even theoretically convincing should account for behaviour of that kind as well as for cases where obviously visual stimuli are available up to a point.

Mr. James Fisher. There is very little left to say, but I would like to make a remark about homing. When a fairly experienced human being is in a maze, he starts by random movements in various unco-ordinated directions; and when he finds that these meet with no success, he begins to guide and direct his movements, and in effect to plan them, and usually ends up in accepting the principle of always turning in one direction. This principle, in most cases, will succeed in bringing him to the middle or the beginning of the maze. But if he finds himself, through continuing to turn in one direction, coming back to a place at which he has been before, he takes a new turn, and then turns as before. If he is systematic, he invariably hunts the maze out to the end. He is able to do this because mazes have walls.

Experienced animals may be able to do a similar operation, not only if they 'know the map', but also if, in the absence of a map imprinted in their minds (that is, if they are in a place where they have never been before), they understand some of the principles of geography—for instance, the nature of coasts and rivers, and mountain ridges, which can take the place of the walls of the maze.

I notice Griffin performed his recent experiments* with adult gannets which he took from Bonaventure Island. They must have been five years old, and had probably learned some of the principles of geography and the 'map' of the Gulf of St. Lawrence. It is conceivable that the gannets may have simply applied some general principles of geography in hunting down the unknown area in which they were released, until they got to the Gulf of St. Lawrence—which most of them did. It is very interesting to see that the original movements of the gannets round the starting-place were very much haphazard. They kept doubling back on their flight: but when they got a bit further away from the starting-place, they began operating in straight lines with very occasional

* *Science* 107: 347–9.

sudden turns. This leads me to think that the principle of operating on a deliberate bias might be one of the methods by which birds can hunt their way out of an unknown country, in a more efficient way than by doing the theoretical spiral travelling, which has been shown to be very wasteful of energy and time.

I only put this forward as rather an ill-formed idea, but it does seem reasonable. It might be applied to Lockley's shearwater which got back to the west coast of Wales in a fortnight. If the shearwater released at Venice had operated on the principle of going along a right-handed coast, it would have got to the Bay of Biscay eventually, and once there it would have recognized its normal feeding-ground, and would have found some other shearwaters of the same subspecies, and known where it was. Even if it had taken a left-handed bias, it would have got round to the Bay of Biscay perhaps a week later than it actually did.

If you look at the map of Western Europe, you will see the coast line is arranged in rather straight lines stretching, for the most part, from north-east to south-west. We might, reasonably, be led to think in terms of birds understanding the principle of this arrangement of the coast, so that when they come to it, even if it is a part with which they are not familiar, they can operate, hunting along in one direction. If they meet with no success in this direction, they could hunt the other until they find a place familiar to them.

Dr. M. H. Pirenne. The absolute sensitivity of some sense organs is very high. For instance, about 100 quanta of green light striking the cornea of the human eye are sufficient to produce a stimulation of the retina and to make the observer see a dim flash of light—under special conditions, including complete dark-adaptation. The number of quanta actually absorbed by the retinal rods, that is, the number acting upon the nervous system to produce a threshold stimulation, is then about 10, or less than 10 (but more than 1). Since these quanta are absorbed each in a different rod, it follows that one rod must be able to respond to only 1 quantum. This quantum reacts, in the primary photochemical reaction, with one single molecule of visual purple. The natural physical limit of one quantum and one molecule is thus reached in the case of the sensitivity of a retinal rod—though not in the case of the organism as a whole.

In terms of energy, the quantities of light involved are about 4×10^{-10} erg at the cornea: the energy necessary to lift a pea to a height of one inch, transformed into light energy, thus should be sufficient to give a faint impression of light to all the men who ever lived. One single quantum ($\lambda=0{\cdot}5\mu$) has an energy of about 4×10^{-12} erg. This is still about 100 times greater than the thermal energy of one molecule at ordinary temperature, mentioned by Dr. Wilkinson. The retina is not sensitive to its own thermal agitation.

In the case of the human ear, the sensitivity is also very high, of the order of 10^{-9} erg per second, or even less, in the most sensitive subjects. The situation here is rather complicated and deserves further study, but it appears that the sensitivity of the end organs of the ear comes close to the limit set by Brownian agitation. In connection with hearing, one may perhaps mention also the great sensitivity to time-differences which is observed in the process of locating certain sources of sound by binaural hearing. The organism reacts to a difference of phase in the sound waves reaching the two ears, and this corresponds to a time difference of 10^{-4} second, or possibly less, in some cases.

It follows that in discussing possible sensory mechanisms to explain bird migration, very high sensitivity cannot *a priori* be ruled out, since it is established that certain sense organs have an extraordinary high sensitivity. The above examples, however, refer to the absolute threshold. The differential sensitivity of the human eye, at its best, *i. e.* at high intensities, is only about one per cent. That is, two similar sources of light having intensities differing by

less than one per cent. will appear as having the same brightness. Needless to say, at these intensities, a difference of one per cent. corresponds to very large numbers of quanta striking the eye : 10^4, or much larger numbers. In the case of the ear the differential threshold is higher than for the eye, it is of the order of 10 per cent. under the best conditions.

We do not seem to know of sensory mechanisms capable of detecting the small *differences* of stimulus intensity discussed by Dr. Wilkinson. The conclusion, that it is improbable that the organism detects and uses such differences for guiding its behaviour, seems therefore to be justifiable.

With regard to the visual powers of birds, these may be very great, greater than those of men. It is, however, difficult to gain definite information even about simple visual abilities of these animals. For instance, while studying the vision of the owl, we tried, the late Professor Hecht and I, to determine its absolute threshold. Various considerations show that the owl may be able to see a light, say 10 times dimmer than the dimmest we can see ; so that a dark night may appear to the owl as a night 10 times brighter would appear to us. Direct measurements were not possible, however, because, when everything was ready, the owl would not even look at the test spot of light prepared for him, and, in fact, seemed to have lost all interest in the experiments.

The remarkable structure of the retina of birds suggest, for instance, that some day-birds may see finer details and finer colour differences than we do. It is possible that birds can, so to speak, gather through their eyes much more information than we could if we were in their place. Such suggestions, however, are particularly difficult to verify directly by experiments.

Concerning the possible use of infra-red radiation in vision, the above-mentioned investigation on the long-eared owl by Hecht and myself has shown that the spectral sensitivity curve of the owl is a rod curve. It is similar in shape and position in the spectrum to the rod sensitivity curve of man (night vision). The sensitivity becomes very low at the extreme red end of the spectrum. Extrapolation of the curve shows that even very large amounts of near infra-red radiation ($\lambda = 1\mu$) are unlikely to produce a response. This has been verified experimentally in this particular owl using the contraction of the pupil as an index of response. No contraction of the iris of the owl could be observed when using an amount of infra-red energy equal to about 5×10^6 times the amount of green light energy which produces an easily perceptible contraction of the iris.

The possibility, in some animal species, of a certain amount of displacement of the sensitivity curve towards the infra-red is of course not excluded by these experiments. In the case of infra-red of longer wave-lengths (λ = a few μ) such as is emitted, for instance, by a body at 40° C., it is, however, hard to believe that ordinary vertebrate eyes can be sensitive to it. Direct experiments on the eye of the tawny owl by Matthews and Matthews failed to show any response. Moreover, the water in the eye media absorbs such radiation strongly—as was also demonstrated directly by these authors. Finally, it must be borne in mind that such infra-red radiation fills the eye itself on account of the eye being at blood temperature. The eye of the owl forming an image of a mouse with the radiation emitted by the mouse itself would, therefore, be functioning in the same way as a camera forming the image of a red-hot poker in a dark room, the camera itself being at the temperature of red heat.

Positive evidence of a really clear-cut nature appears to be lacking with regard to the vision of infra-red by birds. On account of the negative evidence available, and of the theoretical objections, the view that birds may be guided by infra-red radiation in their migrations seems to remain problematical.

(Details and bibliography on the above problems will be found in Pirenne, M. H., *Vision and the Eye*, London 1948.)

Dr. R. G. Newton. There seems to be little doubt that Yeagley's claims for navigation by the use of Coriolis forces and by movement through a magnetic

field are false, and there is no doubt that his paper contains many obscurities, or that his interpretation of the results is unsound, but I am not happy about the implicit suggestion, made by earlier speakers, that *all* of Yeagley's work should be disregarded. If his data are examined statistically, the distribution of recovery-points is found to be significantly non-random, and this feature clearly requires explanation.

There may be many ways of explaining this non-random distribution, and Dr. Thorpe has suggested one of them, *i. e.* that selective recovery of the birds may have occurred, and Yeagley seems to have taken no steps to guard against this. On the other hand, there may be some truth to be learnt from Yeagley's work. If he is wrong about the use of Coriolis forces, he may still be right about navigation by estimation of the geographical latitude, and Dr. Wilkinson has suggested how the elevation of the sun might be used for this purpose. Experiments like Yeagley's can only be done in North America, and it would, therefore, be very interesting and valuable if Yeagley would carry out another experiment incorporating the following new features. In the first place, control birds should be used ; for example, birds trained in Texas and in Pennsylvania could be released in random sequence from the release points around Kearney, and their relative numbers among the recoveries would show whether Pennsylvania birds did better than those from Texas, even though selection on a geographical basis, which might possibly be unavoidable, had occurred among the recoveries. The second desirable feature would be the use of more lofts ; two birds found one or other of the two lofts placed at Kearney, but they may have done this by random searching. If several other identical lofts were placed at intervals in the surrounding country, at distances up to (say) twice that of the release points, the probability of random discovery of a loft could be learnt.

My second object in speaking tonight is to encourage further thought on the important subject of discovering the route taken by the birds, and to suggest two ways of making the bird supply this information. Lack and Lockley released a Shearwater at Start Point, and it returned to Skokholm in 10 hours, taking a north-westerly course if it returned by the direct route, or one south of west at first, followed by north, if it returned by sea. Suppose the bird had a ' micro-sunshine-recorder ', with moving recording paper which travelled vertically, fixed on its back, and pointing backwards with (say) 150° field of view. If the bird had been released on the morning of a cloudless day, its actual direction of flight could be known at all times unless it had flown in a ' spiral ' course or did much random searching, the record being interrupted whenever it flew substantially towards the sun. If used on a Puffin, the record would stop when the bird reached its burrow, and hence the precise time of return would also be known. The device could use a modern lady's watch as the driving mechanism and, if made on the same scale, might not embarrass the bird.

The other suggestion would not provide such useful information but it might, nevertheless, be of some value. Wild birds return home at a rate much less than their possible speed of flight and it has frequently been assumed that they fly vigorously in random directions until at last they arrive home. On the other hand, Griffin describes a herring-gull which dallied for four days on Lake Ontario, and may have travelled more or less directly all the time. In these two contrasts the numbers of wing-beats taken would probably be very different, and a device, analogous to a cyclometer, which counted the wing-beats, might distinguish between the two types of behaviour. Such a device could certainly be made very small and light, and need not actually touch the wings.

Dr. THORPE. Firstly, I would like to ask Dr. Pirenne whether I am right in assuming that the existence of oil droplets in the eye is in no way an indication of infra-red vision.

With regard to migration to the small oceanic islands mentioned by Mr. Tucker, Griffin has considered that problem and has suggested that the characteristic wave pattern and cloud formation formed by oceanic islands may be of importance, such islands often cast a kind of wave 'shadow' visible, perhaps, a hundred miles away, and the cloud formation over the island might be visible for an even greater distance.

I agree that the perception of relatively constant temperature and other differences between air masses in a given region, the regularity of the winds, and so on, probably provide very important methods of orientation for some birds. I suggest that that kind of evidence may be valuable not only to birds migrating in the air, but also to penguins migrating on the surface of the sea which may recognize their position by means of the physical characteristics of the water. It is very difficult for human beings to think of all these possible means of orientation.

I think those are the main points I have in mind, except that I would like to ask Dr. Landsborough Thomson whether there are examples of young birds which take an east-west direction when travelling alone on the autumn migration.

Dr. Pirenne. The presence of coloured filters, such as the red globules present in the cones of certain retinae, does, of course, decrease the sensitivity to the radiations which the filters absorb. It does not, however, in any way increase the sensitivity of the corresponding cones to the radiations transmitted, and the presence of such filters does not even imply necessarily that the cones are sensitive to all the radiations which the filters can transmit.

Dr. Landsborough Thomson. It is rather difficult to answer that on the spur of the moment. There is, for instance, a lot of migration of young starlings before the autumn and they often fly on a more or less east to west line—at least not necessarily from north to south.

TROPICAL FUNGI.—III. NEW SPECIES AND REVISIONS

By C. G. Hansford, M.A., F.L.S.

Note.—The Family names in square brackets on the right of some species indicate the Families to which host-plants belong; the several numbers refer to Hutchinson's *Families of Flowering Plants*, I. & II., 1926, 1934.

The present paper is a continuation of No. II in this series, published in *Proc. Linn. Soc. Lond.* **159**, pp. 21–42, 1947, and deals with new species found in the National Herbarium, Pretoria, together with a number of others requiring revision, as determined from specimens found in that Herbarium. The numbering of species is continued from the previous papers in this series.

100. **Schiffnerula Hippocrateae** Hansf., sp. n.

Plagulae amphigenae plerumque hypophyllae, atrae, usque ad 3 mm. diam., subdensae vel tenues, saepe confluentes, leves. *Mycelium* ex hyphis subrectis, radiantibus, brunneis, 4–6 μ crassis (cellulis plerumque 20–30 μ longis), laxe ramosis, demum in centro plagularum dense ramosis compositum. *Hyphopodia* alternata vel dispersa, hemisphaerica vel ovata, integra, continua, 9–11 μ diam. *Conidia falcata* pauca vel numerosa, brunnea utrinque pallidiora, apice rotundata, basi subapiculata, 3-septata, vix constricta, 26–34 × 7–10 μ. *Conidia sarcinelliformia* subglobosa, muriformia, opace atrobrunnea, levia, usque ad 35 μ diam. *Perithecia* laxe dispersa, sessilia, subglobosa, usque ad 90 μ diam., interdum connata et majora, brunnea, pallidescentia; paries

parenchymaticus, unistratosus, in maturitate cellulis secedentibus et in muco natentibus. *Asci* usque ad 20, plerumque 10–12, globosi, sessiles, circa 25 μ diam. (immaturi). *Sporae* maturae non visae.

Hab. in foliis *Hippocrateae velutinae*, Sierra Leone: Mabang, Ribi, 27.xi.1936, *F. C. Deighton, M 2440* (typus), *M 1026*; Mafore, Samu, 2. ii. 1939, *Deighton, M 1874*; Njala, Kori, 18. i. 1938, *Deighton, M 1524*; Port Loko, 17. ii. 1938, *Deighton, M 1609*.

None of these specimens has been found to contain ripe perithecia, but in view of the fact that no *Schiffnerula* has hitherto been described on this family, it is considered that the present collections must represent a new species.

101. **Schiffnerula Ricini** Hansf., sp. n.

Plagulae amphigenae, subdensae, atrae, leves, orbiculares, usque ad 3 mm. diam., vel confluentes. *Mycelium* ex hyphis brunneis, flexuosis, 4–5 μ crassis (cellulis plerumque 15–20 μ longis), irregulariter ramosis, laxe vel subdense reticulatis compositum. *Hyphopodia* alternata vel dispersa, hemisphaerica, integra, continua, 5–8 μ diam. *Conidia falcata* numerosa, fusoidea, apice rotundata, basi subapiculata, 3-septata, leniter constricta, brunnea utrinque pallidiora, 25–33 × 7–8 μ. *Conidia sarcinelliformia* pauca vel numerosa, subglobosa, opace atrobrunnea, muriformia, usque ad 30 μ diam. *Perithecia* numerosa, subglobosa, brunnea, usque ad 70 μ diam. et ad 40 μ alt.; paries unistratosus, parenchymaticus, superne in maturitate cellulis secedentibus et in muco natentibus. *Asci* usque ad 10, in ordine maturescentes, ovati, aparaphysati, 8-spori circa 35 μ diam. *Sporae* conglobatae, oblongae, utrinque rotundatae, 1-septatae, leniter constrictae, leves, pallide brunneae, 16–19 × 7–9 μ, cellula superiore leniter crassiore.

Hab. in foliis *Ricini communis*, Sierra Leone: Songo, Colony, 28. xi. 1936, *F. C. Deighton, M 1255* (typus); Tombo, Colony, 2. xii. 1936, *Deighton, M 1256*; Kalangba, Gorahun, 29. i. 1939, *Deighton, M 1786*; Newton, Colony, 16. xi. 1934, *Deighton, M 658*.

102. **Schiffnerula Scopariae** Hansf., sp. n.

Plagulae amphigenae, atrae, leves, densae, subcrustosae, usque ad 3 mm. diam. vel late confluentes. *Mycelium* ex hyphis atrobrunneis, subrectis vel flexuosis, 5–7 μ crassis (cellulis plerumque circa 15 μ longis), irregulariter denseque ramosis compositum, in centro plagularum subsolidum. *Hyphopodia* alternata vel laxe dispersa, continua, hemisphaerica, integra 6–9 μ diam. *Conidia falcata* numerosa, fusoidea, apice rotundata, basi subapiculata, 3-septata, haud constricta, levia, brunnea, utrinque pallidiora, 28–35 × 7–9 μ. *Conidia sarcinelliformia* numerosa, subglobosa, muriformia, levia, opace atrobrunnea, usque ad 30 μ diam. *Perithecia* numerosa, subdense dispersa, subglobosa, usque ad 120 μ diam., et ad 50 μ alt., brunnea, levia, sessilia; paries unistratosus, parenchymaticus, demum superne mucoso-diffluens. *Asci* circa 8, globosi, sessiles, aparaphysati, circa 40 μ diam. *Sporae* 8, conglobatae, dilute brunneae, oblongae, utrinque rotundatae, 1-septatae, constrictae, leves, 17–19 × 7–9 μ, cellulis subaequalibus.

Hab. in foliis *Scopariae dulcis*, Sierra Leone: Port Loko, 17. i. 1938, *F. C. Deighton, M 1606*; Songo, Colony, 27. xi. 1936, *Deighton, M 1257*; Waterloo, Colony, 1. xii. 1936, *Deighton, M 1258* (typus); Mobai, Mandu, 20. x. 1939, *Deighton, M 2124*.

103. **Schiffnerula Spigeliae** Hansf., sp. n.

Plagulae amphigenae, atrae, leves, usque ad 1 mm. diam., subdensae et plerumque late confluentes. *Mycelium* ex hyphis brunneis, subrectis vel flexuosis, 5–6 μ crassis (cellulis plerumque 20–25 μ longis), irregulariter ramosis,

primo laxe, demum in centro dense reticulatis compositum. *Hyphopodia* alternata vel dispersa, hemisphaerica, integra, 8–11 μ diam., continua. *Conidia falcata* numerosa, fusoidea, apice rotundata, basi apiculata, 3-septata, haud constricta, brunnea, utrinque pallidiora, 25–32×8–10 μ. *Perithecia* dense dispersa, depresso-globosa, brunnea, usque ad 80 μ diam. et ad 40 μ alt., levia; paries unistratosus, parenchymaticus, in maturitate superne mucoso-diffluens. *Asci* usque ad 8, in successione maturescentes, aparaphysati, globosi vel ovati, 8-spori, circa 30 μ diam. *Sporae* maturae non visae.

Hab. in foliis *Spigeliae Anthelmiae*, Sierra Leone: Newton, Colony, 29. xi. 1938, *F. C. Deighton, M 1259* (typus); Njala, Kori, *Deighton, M 1349*; Kenema, Nongowa, *Deighton, M 1433.*

104. **Schiffnerula Solani** Hansf., sp. n.

Plagulae amphigenae, plerumque epiphyllae, atro-griseae, tenues, leves, usque ad 3 mm. diam., vel numerosae lateque confluentes. *Mycelium* ex hyphis brunneis, sinuoso-flexuosis, 4–6 μ crassis, (cellulis plerumque 15–20 μ longis), irregulariter denseque ramosis, dense reticulatis compositum. *Hyphopodia* alternata, hemisphaerica, continua, integra, 6–8 μ diam. *Conidia falcata* fusoidea, apice rotundata, basi subapiculata, 3-septata, vix constricta, brunnea, utrinque pallidiora, 28–35×8–11 μ. *Conidia sarcinelliformia* pauca, dispersa, subglobosa, opace atro-brunnea, levia, usque ad 35 μ diam. *Perithecia* numerosa, subglobosa, dilute brunnea, levia, usque ad 75 μ diam. et circa 50 μ alt., sessilia; paries unistratosus parenchymaticus, in maturitate superne mucoso-diffluens. *Asci* 4–8, in successione maturescentes, ovati vel globosi, sessiles, 8-spori, aparaphysati, circa 30 μ diam. *Sporae* conglobatae, oblongae, utrinque rotundatae, 1-septatae, leniter constrictae, leves, dilute brunneae, 16–20×7–9 μ, cellula superiore leniter crassiore.

Hab. in foliis *Solani Melongenae*, Sierra Leone: Madonke, Colony, 9. xii. 1936, *F. C. Deighton, M 1185* (typus); Mabang, Ribi, 27. xi. 1936, *Deighton, M 1181*; Taiama, Nimi Koro, 9. xii. 1937, *Deighton, M 1421*; Bo, Kakua, *Deighton, M 1322*; Rotifunk, Bumpe, *Deighton, M 1187*; Bradford, Ribi, *Deighton, M 1186*; Lumley, Colony, *Deighton, M 1184*; York, Colony, *Deighton, M 1183*; in foliis *S. macrocarponis*, Sierra Leone: Port Loko, *Deighton, M 1798*; Taiama, Kori, *Deighton, M1510*; in foliis *S. duplosinuati*, Taiama, Kori, *Deighton, M1509.*

105. **Domingoella Deightoni** Hansf., sp. n.

Mycelium in plagulis *Schiffnerulae* parasitans, ex hyphis hyalinis vel dilutissime griseis, 2–3 μ crassis, laxe irregulariterque ramosis, indistincte septatis, exhyphopodiatis compositum. *Conidiophora* dense stipata, erecta, continua, simplicia, 10–50 μ longa, recta vel varia curvata. *Conidia* terminalia, singula, globosa, atro-brunnea, continua, 10–14 μ diam., basi apiculata, levia.

Hab. in plagulis *Schiffnerulae* spec. in foliis *Lippiae adoensis*, Sierra Leone: Kamaranka, Sanda Kamaranka, *F. C. Deighton, M 2408* (typus).

The hyphae closely invest those of the host and ramify loosely between them, forming at short intervals erect branches which act as conidiophores, bearing each a single terminal conidium. The dark-brown globose conidia have each a small basal apiculus, often lighter in colour and about 3 μ diam. and up to 3 μ long. The same species occurs in the following collections from Sierra Leone:—

On *Sarcinella* stage of *Schiffnerula* sp. on *Lannea Afzelii*, Njala, Kori, *Deighton, M 944*; Port Loko, *Deighton, M 1908*;

On *Sarcinella* stage of *Schiffnerula Hippocrateae* on *Hippocratea*, Mafore, Damia, *Deighton, M 1874.*

106. IRENOPSIS CURVATA (Yates) Stevens in Ann. Myc. **25**, p. 437, 1927.

Colonies epiphyllous, very numerous and punctiform, dense, minute, up to

1 mm. diam. with central perithecia, smooth. Mycelium of dark brown substraight to somewhat crooked hyphae, 7–8 μ thick, the cells mostly about 20 μ long, branching opposite or irregular at 30–90°, closely reticulate-radiating, almost solid in the centre. Capitate hyphopodia alternate or unilateral, antrorse, straight or bent, 15–22 μ long; stalk cell widely cuneate to cylindric, straight or bent, 3–7 μ long; head cell widely clavate to piriform, entire, widely rounded at apex, sometimes subglobose, straight or antrorse-bent, 12–15 × 8–11 μ. Mucronate hyphopodia scattered amongst the capitate, opposite or alternate, ampulliform with short neck 3–4 μ thick, more or less bent, 12–18 × 6–8 μ. Mycelial setae none. Perithecia often single and central, or in close central groups, black, globose, slightly verrucose, up to 160 μ diam., with about 6 spreading or erect setae arising from the upper half, up to 140 μ long, translucent pale brownish, continuous, straight in the lower part, spirally twisted or tightly contorted near the obtuse apex, smooth, 7–9 μ thick, the wall 2–3 μ thick. Spores dark brown, cylindric to slightly ellipsoid with rounded ends, 4-septate, constricted, 31–38 × 13–15 μ (av. 35 × 14 μ)—all the spores measured were those from which colonies had originated.

On unknown host, Samar, Philippines: re-described from *Philipp. Bur. Sci. 24642* (part of the type collection).

[Family 1. Magnoliaceae.]

107. MELIOLA MAGNOLIAE Stevens in Illin. Biol. Monogr. **2**, p. 55, 1916.

Colonies hypophyllous, irregular or orbicular, black, rather thin, almost smooth, up to 20 mm. diam. Mycelium of dark brown substraight hyphae 5–6 μ thick, branching usually opposite at 45–90°, loosely reticulate. Capitate hyphopodia alternate or up to 5 per cent. opposite, 23–35 μ long, often irregularly bent; stalk cell cylindric 5–11 μ long, usually straight; head cell cylindric, from substraight to irregularly bent and often more or less uncinate, 17–25 × 6–9 μ, entire with rounded to somewhat pointed apex. Mucronate hyphopodia scattered, opposite or alternate, subcylindric, conoid to ampulliform, up to 24 μ long. Mycelial setae few, scattered, erect, black, straight or somewhat bent but not uncinate, opaque, up to 700 μ long by 7–9 μ thick, apex in all mature setae seen 2–3-dentate up to 15 μ long. Perithecia scattered black globose verrucose, up to 195 μ diam. Spores dark brown, cylindric to slightly ellipsoid, ends rounded, 4-septate, deeply constricted, 45–52 × 19–22 μ.

On *Magnolia portoricensis*, Porto Rico: re-described from *F. L. Stevens 4738* (the type collection).

[Family 11. Lauraceae.]

107. MELIOLA MARTINIANA Gaill., Le Genre Meliola, p. 68, 1892. Syn. IRENOPSIS MARTINIANA (Gaill.) Stevens in Ann. Myc. **25**, p. 437, 1927.

Examination of *Rabh.-Wint.-Pazschke, Fungi. europ. 3852* in Herb. Pretoria has shown no perithecia present, but a few scattered mycelial setae, erect, simple, straight, obtuse, up to 400 × 9–10 μ; this necessitates the re-assignment of the species to *Meliola*.

[Family 120. Melastomaceae.]

108. MELIOLA MOURIRIAE Ciferri in Ann. Myc. **29**, p. 284, 1931.

In the Herb. Pretoria specimen of the type collection, *Ciferri, Micofl. doming. 24*, the capitate hyphopodia are opposite or up to 30 per cent. alternate; the mycelial setae are 500–700 × 8–9 μ, not 10–12 μ thick as given in the original description; the spores found varied 38–45 μ in length, not 44–50 μ as given by Ciferri.

[Family 126. Guttiferae.]

109. MELIOLA MANGOSTANA Sacc. in Bol. Orto Bot. Univ. Napoli, **6**, p. 42, 1921.

Stevens in Ann. Myc. **25**, p. 457, 1927, placed this species as a member of his new genus *Irenina*, though he stated that its position was rather doubtful in view of

the presence of mycelial setae on *Baker, Fungi Malay. 453*, one of the two specimens quoted.

I have examined *Baker, Fungi Malay. 450* on *Garcinia kydia*, Singapore, in the Herbarium of the Royal Botanic Gardens, Peradeniya, labelled *Meliola Kydia* Sacc. :—

Colonies amphigenous, black, dense on the upper surface but not crustose, thinner on the lower surface, up to 4 mm. diam., or confluent over most of the leaf. Mycelium of straight dark brown hyphae 8–9 μ thick, the cells mostly about 20 μ long, branching opposite at 60–90°, densely reticulate. Capitate hyphopodia alternate, at wide angles, 17–25 μ long; stalk cell 3–8 μ long, cylindric to widely cuneate; head cell subglobose to cylindric-clavate, broadly rounded at the apex, entire, 11–17 × 9–14 μ. Mucronate hyphopodia few, scattered, alternate or opposite, mixed with the capitate, ampulliform to subconoid, straight or bent, 15–26 × 8–10 μ. Mycelial setae numerous, erect, black, straight, simple acute, 500–1100 × 10–11 μ. Perithecia scattered, black globose, up to 280 μ diam., verrucose. Spores dark brown, cylindric with rounded ends, 4-septate, constricted 48–60 × 20–24 μ.

Baker, Fungi Malay. 453 on *Garcinia*, Singapore, Herb. Pretoria has the following characters :—

Colonies epiphyllous, thin effuse spreading over most of the leaf, black. Mycelium of substraight dark brown hyphae 8–9 μ thick, the cells mostly 20–30 μ long, branching usually opposite at 45–60°. loosely reticulate. Capitate hyphopodia alternate, at wide angles, usually straight, 18–25 μ long; stalk cell cylindric 5–8 μ long; head cell cylindric-clavate, widely rounded at apex, 14–19 × 8–12 μ. Mucronate hyphopodia few, alternate, scattered amongst the capitate, ampulliform, more or less bent, 22–28 × 8–10 μ, the neck short, 3–4 μ thick. Mycelial setae fairly numerous, erect, straight, opaque black, simple, up to 800 × 9–11 μ, gradually attenuate to the obtuse apex 5–6 μ thick. Perithecia loosely scattered, black, globose, verrucose, up to 240 μ diam. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 39–50 × 17–20 μ.

It is, therefore, evident that neither of the two specimens quoted by Stevens, *l. c.*, has the characters of *Irenina*. *Baker, Fungi Malay. 450* is very close to *M. Garciniae* Yates, but differs from this in its acute setae; the West-African collections of Deighton on *Pentadesma butyracea* have been referred to *M. Garciniae*, having the typical obtuse setae. For the present, therefore, until a wider range of specimens becomes available, it seems best to retain *M. kydia* Sacc. as distinct from *M. Garciniae* Yates and distinguished mainly by the acute setae. *Baker, Fungi Malay. 453* differs from *M. Garciniae* in rather narrower capitate hyphopodia and somewhat smaller spores; the colonies are also thinner, and these differences are regarded as hardly sufficient to distinguish specifically from *M. Garciniae*. In my opinion the specimen is best regarded as **M. Garciniae** Yates var. **mangostana** (Sacc.) Hansford comb. n. (Syn. *Meliola mangostana* Sacc.).

The above arrangement does not include the Uganda specimens *Hansford 2581* on *Symphonia gabunensis*, which show no mycelial setae and therefore are truly classified as *Irenina* :—

110. **Irenina Symphoniae** Hansf., sp. n.

Plagulae epiphyllae, tenues, atrae, orbiculares, 1–8 mm. diam. *Mycelium* ex hyphis atrobrunneis, subrectis vel flexuosis, 7–9 μ cr., alternatim vel opposite ramosis, laxe reticulatis compositum, cellulis 20–35 μ longis. *Hyphopodia capitata* alternata, plus minusve antrorsa, 20–35 μ longa; cellula basali cylindracea vel crasse cuneata, recta vel curvula, 20–35 μ longa; cellula apicali ovata, clavata vel subirregulari, 13–20 × 12–16 μ. *Hyphopodia mucronata* pauca, dispersa, opposita, breve ampullacea. *Setae* nullae. *Perithecia* dispersa,

globosa, atra, verrucosa, usque ad 170 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, leves, 40–51 × 13–18 μ.

Hab. in foliis *Symphoniae gabunensis*, Uganda : L. Nabugabo, Masaka, *Hansford 2581* (ex *P. Chandler 1951* in Herb. Bot. Uganda), (typus).

[Family 133. Malpighiaceae.]

111. **Irenopsis Malpighiae** Hansf., sp. n.

Plagulae epiphyllae, atrae, densae, leves, usque ad 2 mm. diam. *Mycelium* ex hyphis undulatis vel sinuosis, atrobrunneis, 7–8 μ crassis, (cellulis plerumque 15–20 μ longis), opposite ramosis (45–90°), dense reticulatis compositum. *Hyphopodia capitata* alternata, rarissime opposita, recta vel saepe antrorse-curvata, 15–24 μ longa, cellula basali cylindracea, 5–9 μ longa, cellula apicali clavata, irregulariter angulosa vel sublobata, saepe anguste antrose-curvata, 11–17 × 8–13 μ. *Hyphopodia mucronata* pauca, dispersa, opposita vel alternata, ampullacea vel conoidea, 15–20 × 7–9 μ, collo brevi 4–5 μ crasso. *Setae myceliales* nullae. *Perithecia* laxe dispersa, subglobosa, atra, verrucosa, usque ad 180 μ diam., sursum setis 4–7, erecto-patentibus, atris, rectis vel leniter incurvatis, 2-septatis, simplicibus, obtusis, usque ad 80 μ longis et 7–9 μ crassis ornata. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 36–42 × 16–19 μ, rarius utrinque subapiculatae.

Hab. in foliis *Malpighiae glabrae*, Costa Rica : Grecia, *Sydow*, in consortio *Asterinae indecorae* Syd., in *Sydow, Fungi exot. exs. 681* distributae. (Typus in Herb. Pretoria).

112. Irenina malloticola Yamamoto in Trans. Nat. Hist. Soc. Formosa, **30**, p. 415, 1940.

Specimens from the following exsiccata from the Philippines appear to belong to this species : *Philipp. Bur. Sci. 24650* on *Mallotus* sp., Catubig R., Samar, and *Philipp. Bur. Sci. 24049* on *M. ricinoides*, Laguna, Luzon. Both were issued under the name *Asterina perpusilla* Syd.

[Family 136. Euphorbiaceae.]

113. **Meliola janeirensis** Hansf., sp. n.

Plagulae epiphyllae, atrae, tenues, usque ad 3 mm. diam. vel late confluentes. *Mycelium* ex hyphis atrobrunneis, subrectis, 6–8 μ crassis (cellulis plerumque 20–30 μ longis), opposite ramosis (45–90°), laxe vel subdense reticulatis compositum. *Hyphopodia capitata* alternata vel usque ad 40 per cent. opposita, plus minusve antrorsa, recta vel leniter curvata, 12–18 μ longa, cellula basali cylindracea, 2–5 μ longa, cellula apicali globosa vel piriformi, integra, 10–14 × 9–12 μ. *Hyphopodia mucronata* numerosa, dispersa, opposita vel alternata, ampullacea, curvata, 15–20 × 7–10 μ, collo brevi 3 μ crasso. *Setae myceliales* laxe dispersae et circum perithecia aggregatae, erectae, atrae, rectae, usque ad 300 × 8 μ, apice breviter irregulariter dentatae ad 8 μ. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 170 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, leniter constrictae, 39–46 × 14–17 μ [average :] 40 × 16 μ.

Hab. in foliis *Crotonis* spec., Rio de Janeiro, Brazil, July 1887, *Ule* (*Rabh.-Wint.-Pazschke, Fungi europ. 3848*, sub *M. bicorne* Wint. var. *constipata* Speg.) (Typus in Herb. Pretoria).

The type of var. *constipata* Speg. was on an unknown legume, Paraguay. It is rather close to *M. brevidentata* Syd. but has larger spores.

114. Meliola manihoticola P. Henn. in Hedwigia, **43**, p. 364, 1904.

Colonies epiphyllous, rarely also hypophyllous, black, orbicular, scattered, up to 1 mm. diam., subdense. Mycelium of substraight dark brown hyphae

7–8 μ thick, the cells mostly about 20 μ long, branching opposite or irregular at 45–90°, closely reticulate. Capitate hyphopodia alternate or up to 10 per cent. opposite, at wide angles, 12–16 μ long; stalk cell cylindric 1–4 μ long; head cell globose entire 10-12 μ diam., sometimes longer than wide. Mucronate hyphopodia mixed with capitate, opposite or alternate, ampulliform, more or less bent, 15–24 × 6–9 μ, neck elongate, 3–5 μ thick. Mycelial setae mostly grouped around the perithecia, thinly scattered over the rest of the colony, erect, flexuous to widely hamate, rarely straight, simple obtuse 100–160 × 9–11 μ, translucent dark brown and thick-walled, much like the perithecial setae of many species of *Irenopsis*. Perithecia scattered black globose verrucose up to 150 μ diam., not setose. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 31–37 × 12–13 μ.

Re-described from *Ule, Mycoth. brasil. no. 60,* on *Manihot,* in Herb. Pretoria.

115. Meliola sauropicola Yates in Philipp. Journ. Sci. **12**, p. 368, 1917.

Colonies black, amphigenous, rarely caulicolous, 1–3 mm. diam., scattered, rather dense, velvety. Mycelium of substraight to slightly sinuous dark brown hyphae 7–9 μ thick, the cells mostly 30–40 μ long, branching usually opposite at 60–90°, loosely to closely reticulate. Capitate hyphopodia alternate only, at wider angles, straight or slightly bent, 18–30 μ long; stalk cell cylindric to cuneate, 6–13 μ long; head cell subglobose, ovate or widely clavate, entire, 12–20 × 8–13 μ. Mucronate hyphopodia mixed with the capitate, mostly alternate, ampulliform, more or less bent, 15–22 × 7–10 μ, with neck 3–5 μ thick. Mycelial setae mostly grouped around the perithecia erect, straight or somewhat flexuous, not unicinate, black, simple, obtuse, up to 800 × 9–11 μ, attentuate to 4–5 μ at the apex. Perithecia loosely scattered, black globose verrucose, up to 160 μ diam. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 35–44 × 13–15 μ (av. 40 × 14 μ).

Re-described from *Philipp. Bur. Sci. 24705,* part of the type collection, on *Sauropus* sp., Samar, Philippines, in Herb. Pretoria.

[Family 146. Leguminosae.]

116. Meliola polyodonta Syd. in Ann. Myc. **24**, p. 306, 1926, emend. Hansf.

Re-described from *Sydow, Fung. exot. exs. 620,* on undetermined legume, Costa Rica, part of the type collection. Two distinct species of *Meliola* are mixed, and were confused in the original description.

Plagulae amphigenae, plerumque epiphyllae, arachnoideae, tenues, usque ad 4 mm. diam., vel in confluendo multo majores. *Mycelium* ex hyphis atrobrunneis, subrectis vel sinuoso-flexuosis, 5–7 μ crassis, (cellulis plerumque 25–35 μ longis), opposite ramosis (45–90°), laxe reticulatis compositum. *Hyphopodia capitata* alternata (vel circa 0·5 per cent. opposita), plus minusve curvata, 11–18 μ longa, cellula basali cylindracea, 3–7 μ longa, cellula apicali integra, ovata, clavata, saepe curvata, 8–12 × 7–10 μ. *Hyphopodia mucronata* pauca, dispersa, opposita vel alternata, ampullacea, plus minusve curvata, 15–22 × 6–9 μ, collo elongato 3–4 μ cr. *Setae myceliales* laxe dispersae, etiam circum perithecia aggregatae, erectae, atrae, subrectae, sursum rugulosae vel dentibus lateralibus minutis (—3 μ) ornatae, apice similiter dentatae vel usque ad 50 μ 2-furcatae. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 150 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 27–33 × 11–13 μ [average :] 30 × 12 μ.

117. **Meliola Sydowi** Hansf., sp. n.

Plagulae plerumque epiphyllae, subdensae, atrae, 1–4 mm. diam., vel confluentes. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter undulatis, 6–8 μ crassis, (cellulis plerumque 20–30 μ longis), opposite vel irregulariter

ramosis (45–90°), laxe reticulatis compositum. *Hyphopodia capitata* alternata, suberecta, saepe curvata, 15–26 μ longa, cellula basali cylindracea, 4–8 μ longa, cellula apicali irregulariter angulosa vel sublobata, saepe acute curvata, versiformi, 11–15 × 9–17 μ. *Hyphopodia mucronata* in hyphis distinctis evoluta, opposita vel alternata, ampullacea, 15–20 × 8–10 μ, collo elongato 2–3 μ cr. saepe curvato praedita. *Setae myceliales* laxe dispersae, erectae, rectae, atrae, simplices, acutae vel subacutae, leves, usque ad 400 × 7–8 μ. *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 160 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 34–39 × 14–16 μ [average :] 37 × 15 μ.

Hab. in foliis *Leguminosarum* spec. indet., S. Pedro de S. Ramon, Costa Rica, 5. ii. 1925, in consortio *Meliolae polyodontae* Syd. in *Sydow, Fung. exot. exs. 620* distributae (typus in Herb. Pretoria).

This is one of the very few species recorded on Papilionaceae with irregular capitate hyphopodia ; in all characters it is very distinct from the preceding species, with which it occurs in mixed infection in this collection.

118. **Meliola franciscana** Hansf., sp. n.

Plagulae epiphyllae, orbiculares, subdensae, usque ad 2 mm. diam. *Mycelium* ex hyphis atrobrunneis, rectis, 6–8 μ crassis, (cellulis plerumque 20–30 μ longis), opposite ramosis (30–60°), dense reticulatis compositum, in centro plagularum subsolidum. *Hyphopodia capitata* opposita, in congregatione saepe alternata, plerumque recta, suberecta, 12–15 μ longa, cellula basali cylindracea, 2–5 μ longa, cellula apicali globosa vel piriformi, apice late rotundata, integra, 9–12 μ diam. *Hyphopodia mucronata* pauca, plerumque inter hyphopodia capitata intermixta, opposita vel alternata, ampullacea, circa 15 × 9 μ, collo brevi curvato, 3 μ crasso praedita. *Setae myceliales* in mycelio laxe dispersae, etiam circum perithecia aggregatae, erectae, rectae, acutae, simplices, atrae, usque ad 400 × 6–8 μ. *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 160 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 36–41 × 13–17 μ [average :] 38 × 16 μ.

Hab. in foliis *Leguminosarum* spec. indet., S. Francisco, Brazil, Oct. 1884, leg. *Ule* (*Rabh.-Wint. Fung. europ. 3248*, sub *Meliola ludibunda* Speg., distributa). Typus in Herb. Pretoria.

M. ludibunda Speg. was described on an unknown host from Guarapi, Paraguay.

119. Irenopsis toruloidea (Stev.) Stev. in Ann. Myc. **25**, p. 441, 1927.

Colonies amphigenous, mostly hypophyllous, orbicular, 1–4 mm. diam., black, rather dense. Mycelium of dark brown substraight or slightly undulate hyphae 6–8 μ thick, the cells mostly 20–30 μ long, branching usually opposite at 30–90°, rather closely reticulate. Capitate hyphopodia alternate or unilateral, at wide angles, usually straight, 15–25 μ long ; stalk cell cylindric, 3–8 μ long ; head cell cylindric to widely clavate or almost subglobose, entire, 10–17 × 9–12 μ. Mucronate hyphopodia scattered amongst the capitate, alternate, conoid to ampulliform, straight or slightly bent, 13–18 × 7–9 μ, neck short. Mycelial setae none. Perithecia loosely scattered, black, globose, when young verrucose, up to 170 μ diam., when mature with 6–15 erect-spreading black simple setae, up to 80 × 7–8 μ, arising from the upper half ; the setae obtuse and uncinate to tightly coiled at the apex. Spores dark brown, cylindric to subellipsoid with broadly rounded ends, 4-septate constricted, 29–35 × 14–16 μ.

Re-described from part of the type collection, *F. L. Stevens 8394* on *Cassia quinquadrangulata*, Porto Rico, in Herb. Pretoria.

120. IRENINA HYMENAEICOLA (Frag. & Cif.) Stevens in Ann. Myc. **25**, p. 462, 1927.

Colonies epiphyllous black orbicular dense smooth, up to 5 mm. diam. Mycelium of straight dark brown hyphae 6–8 μ thick, the cells mostly 12–20 μ long, branching usually opposite at 45–60°, closely reticulate. Capitate hyphopodia alternate or up to 20% opposite, more or less antrorse, usually straight, 16–23 μ long ; stalk cell cylindric to cuneate, 4–7 μ long ; head cell widely clavate to globose, 12–16 × 10–14 μ, entire. Mucronate hyphopodia numerous, scattered amongst the capitate, opposite or alternate, ampulliform with short wide bent neck. Mycelial setae none. Perithecia few, each on a close solid radiate subiculum of exhyphopodiate hyphae, fimbriate around the edge, flattened globose to somewhat hemispheric on a wide base, never truly globose, black, verrucose, up to 250 μ diam. Spores dark brown, cylindric with broadly rounded ends, 4-septate constricted, 45–54 × 20–24 μ.

On *Hymenaea, Ciferri, Micofl. doming. 75*, part of the type collection, in Herb. Pretoria.

This species is intermediate with *Amazonia*, the species of which genus, however, have usually smooth perithecia covered by a more or less radiating layer of mycelium, whereas the perithecial wall of *I. hymenaeicola* is parenchymatous, with the surface cells about 35–40 μ diam., and bluntly conoid, up to 30 μ high.

121. MELIOLA AETHIOPS Sacc. in Bol. Orto. Bot. Napoli, **6**, p. 41, 1921.

The specimen *Sydow, Fung. exot. exs. 172*, on *Caesalpinia nuga* Lamao, Bataan, Luzon, Philippines, leg. *Merrill*, belongs to this species and not to *M. cylindrophora* Rehm, as originally determined ; the type of the latter is on Saxifragaceae.

122. **Meliola Entadae** Hansf., sp. n.

Plagulae hypophyllae, rarissime etiam epiphyllae, tenues, atrae, subvelutinae, usque ad 3 mm. diam. *Mycelium* ex hyphis atrobrunneis, flexuosis, 4–6 μ crassis (cellulis plerumque 15–20 μ longis), opposite vel irregulariter ramosis, laxe reticulatis compositum. *Hyphopodia capitata* alternata vel usque ad 20% opposita, suberecta, recta vel curvula, 10–14 μ longa ; cellula basali cylindracea, 2–5 μ longa, cellula apicali anguste clavata, integra vel varie deformata, 7–10 × 4–6 μ. *Hyphopodia mucronata* pauca, dispersa, opposita vel alternata, ampullacea vel conoidea, 14–18 × 4–6 μ, collo subrecto 2–3 μ cr. praedita. *Setae myceliales* laxissime dispersae, etiam circum perithecia aggregatae, erectae, rectae, atrae, usque ad 400 × 7 μ, apice 2–3-dentatae (–10 μ). *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 150 μ diam. *Sporae*, atrobrunneae, cylindraceae, utrinque late rotundatae, 4-septatae constrictae, 33–41 × 13–16 μ [average :] 36 × 14 μ.

Hab. in foliis *Entadae gigantis*, San Domingo, *Ciferri, Micofl. doming. 151*, sub *Meliola Teramni* Syd. (Typus in Herb. Pretoria.)

This specimen was originally determined as *M. Teramni* Syd., from which it differs markedly in characters of mycelium and setae. *F. C. Deighton, M 2329* on *Entada africana*, Gofor, Dama, Sierra Leone, is very similar to the above, but differs in that the colonies are epiphyllous and the capitate hyphopodia rather wider, the head cells verging to subglobose. The setae are also obtuse or obtusely dentate to 8 μ, but this may be due to partial immaturity ; for the present *Deighton, M 2329* is included in *M. Entadae.*

123. MELIOLA JURUANA P. Henn. in Hedwigia, **43**, p. 365, 1904.

The following re-description is based on part of the type collection, *Ule 2935*, on *Lonchocarpus*, Amazonia, in Herb. Pretoria :—

Colonies epiphyllous, black, orbicular, rather dense, up to 4 mm. diam., velvety. Mycelium of substraight to slightly flexuous dark brown hyphae 8–10 μ thick, the cells mostly 25–30 μ long, branching opposite at 60–90°, closely reticulate. Capitate hyphopodia alternate or up to 5% opposite, straight or bent, 20–29 μ long ; stalk cell cylindric, 5–9 μ long ; head cell cylindric-clavate, rounded at apex, often sinuous or bent, entire, 13–22 × 9–21 μ. Mucronate hyphopodia mixed with the capitate on a few hyphae, opposite or alternate, ampulliform, more or less bent, 15–23 × 8–10 μ, with rather long bent neck 3–4 μ thick. Mycelial setae rather few, scattered, erect, straight black, up to 200 μ high by 9–11 μ thick at the base, 1–2-dichotomous above, the branches widely reflexed and obtuse, the primary up to 60 μ long. Perithecia scattered black globose verrucose, up to 180 μ diam. Spores dark brown cylindric with widely rounded ends, 4-septate constricted, 43–50 × 17–19 μ.

124. Meliola Inocarpi Stev. in Ann. Myc. **26**, p. 232, 1928.

Stevens' rather fragmentary description is here amplified from part of the type collection, *Baker, Fungi Malay 459*, on *Inocarpus*, Singapore, in Herb. Pretoria :—

Colonies amphigenous, black, orbicular, rather dense, 2–8 mm. diam., often numerous and widely confluent. Mycelium of dark brown substraight hyphae 7–8 μ thick, the cells mostly 25–30 μ long, branching usually opposite at 60–90°, densely reticulate towards the centre. Capitate hyphopodia opposite, slightly antrorse, usually straight, 15–20 μ long ; stalk cell cylindric, 2–5 μ long ; head cell cylindric with rounded apex 12–18 × 7–10 μ, entire. Mucronate hyphopodia numerous towards the centre, mixed with the capitate, opposite, ampulliform, more or less bent, 16–23 × 8–10 μ, neck elongate, 3–4 μ thick. Mycelial setae rather few, scattered, erect, straight, black, simple acute, up to 920 × 9–11 μ, those around the perithecia much shorter. Perithecia scattered loosely, black globose verrucose, up to 190 μ diam. Spores dark brown, broadly ellipsoid with rounded ends, 4-septate, constricted, 40–48 × 19–22 μ.

[Family 169. Urticaceae.]

125. **Irenina Pipturi** Hansf., sp. n.

Plagulae epiphyllae, usque ad 1 mm. diam., atrae, subdensae. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter undulatis, 7 μ crassis (cellulis plerumque 15–20 μ longis), opposite vel alternatim ramosis (45–90°), subdense reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, recta, 20–27 μ longa, cellula basali cylindracea vel cuneata, 5–11 μ longa, cellula apicali late triangulosa, plerumque sub-3-lobata, 14–18 × 11–19 μ. *Hyphopodia mucronata* dispersa, opposita vel alternata, ampullacea, curvata, 15–20 × 6–9 μ, collo 3 μ crasso praedita. *Setae* nullae. *Perithecia* in centro plagularum, atra, globosa, verrucosa, 100–140 μ diam., cellulis parietis rotundato-conoideio usque ad 12 μ alt. *Sporae* atrobrunneae, ellipsoideae, utrinque late rotundatae, 4-septatae, constrictae, 36–43 × 17–19 μ.

Hab. in foliis *Pipturi arborescentis*, Samar, Philippine Is., March 1916, *M. Ramos*, in consortio *Asterinae Pipturi* Syd. in *Philipp. Bur. Sci. 17634*, distributae. (Typus in Herb. Pretoria.)

This species was originally included under *M. triloba* Wint. (*Irenina triloba* (Wint.) Stevens).

126. **Irenina Pileae** Hansf., sp. n.

Plagulae epiphyllae, atrae, orbiculares, usque ad 1 mm. diam., numerosae, leves, densae, haud confluentes. *Mycelium* ex hyphis atrobrunneis, subrectis, 7–8 μ crassis (cellulis plerumque 20–30 μ longis) opposite ramosis (45–90°),

dense reticulatis compositum. *Hyphopodia capitata* alternata, recta vel subcurvata, 20–30 μ longa, cellula basali cylindracea vel cuneata, 5–8 μ longa, cellula apicali clavata vel irregulariter 2–5-lobata, 14–24 × 11–16 μ. *Hyphopodia mucronata* in centro plagularum pauca, alternata, raro opposita, ampullacea vel conoidea, recta vel curvula, 14–20 × 7–8 μ, collo brevi 3–5 μ cr. *Setae myceliales* nullae. *Perithecia* laxe dispersa, atra, globosa, usque ad 230 μ diam., cellulis parietis obtuse conoideis, vel apice in processos obtuse cylindraceo-conoideos, curvatos, usque at 30 μ alt., basi circa 40 μ diam., elongatis. *Sporae* atrobrunneae, cylindraceae vel ellipsoideae, utrinque late rotundatae, 4-septatae, constrictae, 36–45 × 14–17 μ.

Hab. in foliis *Pileae Parietariae*, Arecibo-Lares Road, Porto Rico, 21. vi. 1915, *F. L. Stevens 7232*, sub *Meliola triloba* Wint., distributa. (Typus in Herb. Pretoria.)

This species was originally included under *I. triloba* (Wint.) Stevens, of which the type was described on Cucurbitaceae.

[Family 171. Aquifoliaceae.]

127. **Meliola ilicicola** Hansf., sp. n.

Plagulae epiphyllae, atrae, densae, orbiculares, subvelutinae, usque ad 4 mm. diam. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter undulato-flexuosis, 6–8 μ crassis (cellulis plerumque 20–25 μ longis), opposite vel irregulariter ramosis (45–90°), dense reticulato-intertextis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, recta vel varie curvata, 20–29 μ longa, cellula basali cylindracea vel cuneata, recta vel curvata, 8–13 μ longa, cellula apicali raro cylindraceo-clavata integraque, plerumque irregulariter undulato-curvata vel rotundato-angulosa, 12–18 × 8–15 μ. *Hyphopodia mucronata* pauca, dispersa, alternata vel opposita, curvata, ampullacea, 15–19 × 6–9 μ, collo brevi 4 μ cr. *Setae myceliales* laxe dispersae, erectae, atrae, rectae vel flexuosae, haud uncinatae, simplices, obtusae, usque ad 360 × 7–9 μ, apice 3 μ cr. *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 150 μ diam. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque late rotundatae, 4-septatae, constrictae, 35–43 × 18–21 μ [average :] 38 × 19 μ.

Hab. in foliis *Ilicis montanae*, San Domingo, *Ciferri, Micofl. doming.*, sub *Irenina Lagerheimii* (Gaill.) Stev. (Typus in Herb. Pretoria.)

The mycelial setae are found only in unparasitized colonies, and remove this form from *Irenina Lagerheimii* (Gaill.) Stev. with which it was originally placed by Ciferri ; the spores are also much smaller than those described for this species.

128. Meliola Zizyphi Hansford & Thirumalacher (in press).

A few rather immature colonies of a *Meliola* corresponding to the above were found among those of *Asterina Zizyphiae* Yates (sic !) on *Zizyphus* sp., Mt. Tulaog, Tayabas, Luzon, Philippine Is. in *Philipp. Bur. Sci. 29156*, in Herb. Pretoria.

[Family 194. Rutaceae.]

129. **Meliola Fagarae-martinicensis** Hansf., sp. n.

Plagulae epiphyllae, atrae, velutinae, usque ad 5 mm. diam., subdensae, saepe numerosae confluentesque. *Mycelium* ex hyphis atrobrunneis, subrectis, 7–8 μ crassis (cellulis plerumque circa 30 μ longis), opposite ramosis (60–90°), dense reticulatis compositum. *Hyphopodia capitata* alternata, suberecta, plerumque recta, cylindracea, 20–28 μ longa, cellula basali cylindracea, 3–7 μ longa, cellula apicali cylindracea, apice rotundata, 13–22 × 7–10 μ, raro leniter clavata vel subovata. *Hyphopodia mucronata* in centro plagularum inter hyphopodia capitata interspersa, plerumque opposita, ampullacea, 17–21 × 7–8 μ, collo plus minusve curvato 3–4 μ cr. *Setae myceliales* numerosae, dispersae,

erectae, atrae, rectae, usque ad 650×8–9 μ, apice raro simplices, attenuato-obtusae, plerumque 2–4-dentatae (–10 μ), raro 2-furcatae (–30 μ), ramis dentatis. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 190 μ diam. *Sporae* atrobrunneae, cylindraceae, vel subellipsoideae, utrinque late rotundatae, 4-septatae, constrictae, 36–43×16–18 μ [average :] 40×17 μ.

Hab. in foliis *Fagarae martinicensis*, San Domingo, *Ciferri, Micofl. doming. 50*, sub *Meliola macropoda* Syd. (Typus in Herb. Pretoria.)

It is markedly different in the size of all its parts from *M. macropoda*.

[Family 211. Araliaceae.]

130. Meliola Polysciatis Hansf. in Proc. Linn. Soc. Lond. 1944–45, p. 184, 1946.

On ?*Didymopanax* sp., Minas Geraes, Brazil, *Noack* (in Herb. Pretoria from Engler, and apparently *Noack 669*, mentioned in Ann. Myc. **5**, p. 356, 1907, as determined by H. & P. Sydow) :—

Colonies epiphyllous, black, orbicular, 1–3 mm. diam., dense, subvelvety, the smaller colonies often without setae. Mycelium of dark brown straight hyphae 7–9 μ thick, the cells mostly 20–30 μ long, branching opposite at 30–60°, or often irregular, densely reticulate and in the centre almost solid. Capitate hyphopodia alternate (very rarely, much less than 1% opposite, usually straight or slightly antrorsely bent, 17–22 μ long ; stalk cell cylindric, 3–8 μ long ; head cell ovate to piriform, widely rounded at the apex, entire straight, 12–16×10–11 μ. Mucronate hyphopodia mostly in the centre, mixed with the capitate, opposite or alternate conoid to ampulliform more or less bent, 20–25×7–9 μ, with short neck 3–5 μ thick. Mycelial setae only in the older and larger colonies, when numerous, erect black simple obtuse, broadly uncinate to falcate in upper half, rarely almost straight, up to 450×8–10 μ, attenuate to 4–5 μ at apex. Perithecia scattered black, globose, verrucose, up to 170 μ diam. Spores dark brown cylindric with rounded ends, 4-septate constricted, 40–47×15–17 μ (av. 42×16 μ).

This was placed by Sydow as *M. didymopanicis* P. Henn., from which it differs in the uncinate obtuse setae ; in spite of some differences in mycelium and setae, for the present I place it with the Uganda specimens on *Polyscias fulva*, this being the only species hitherto described on Araliaceae having uncinate obtuse setae.

[Family 205. Anacardiaceae.]

131. **Meliola Anacardii** Zimm. var. **minor** Hansf., var. n.

Plagulae epiphyllae, tenues, atrae, usque ad 4 mm. diam., orbiculares. *Mycelium* ex hyphis atrobrunneis, rectis, 7–8 μ crassis (cellulis plerumque 20–25 μ longis), opposite ramosis (60–90°), laxe reticulatis compositum. *Hyphopodia capitata* alternata, suberecta, recta, 16–20 μ longa, cellula basali cylindracea, 3–6 μ longa, cellula apicali ovata, apice attenuato-rotundata vel subacuta, recta, integra, 11–17×8–11 μ. *Hyphopodia mucronata* pauca, dispersa, opposita vel alternata, ampullacea, curvata vel conoidea, 20–25×7–9 μ, collo 3 μ crasso. *Setae myceliales* laxe dispersae, etiam circum perithecia parce aggregatae, erectae, atrae, rectae, usque ad 360×7–9 μ, apice raro simplices, acutae, plerumque 2–3-dentatae (–8 μ). *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 150 μ diam., cellulis parietis obtuse conoideis. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 35–41×16–19 μ.

Hab. in foliis *Anacardii occidentalis*, Philippine Is., sub *Meliola Anacardii* Zimm., *Philipp. Bur. Sci. 21905* (typus in Herb. Pretoria), *21898*.

This differs from the type in the more pointed hyphopodia and in the smaller spores.

[Family 215. Ericaceae.]

132. Meliola Vaccinii Stevens in Bishop Mus. Bull., Hawaii, **19** p. 30, 1925.

Colonies amphigenous black dense orbicular 1 mm. diam., velvety. Mycelium of dark brown substraight hyphae 7–8 μ thick, the cells mostly 20–25 μ long, branching usually opposite at 60–90°, closely reticulate. Capitate hyphopodia alternate or up to 10% opposite, somewhat antrorse, usually straight, 18–26 μ long ; stalk cell cylindric, 5–9 μ long ; head cell cylindric with rounded apex, usually straight, sometimes narrowly ovate, 12–16 × 8–10 μ. Mucronate hyphopodia not seen. Mycelial setae scattered erect straight or widely arcuate, not uncinate or hamate, black simple obtuse, up to 600 × 9–10 μ thick, abruptly attenuate above. Perithecia closely scattered black globose verrucose, up to 240 μ diam. Spores dark brown cylindric to subellipsoid with rounded ends, 4-septate, 43–48 × 16–18 μ, the central cell often slightly larger than the others.

On *Vaccinium reticulatum*, Hawaii, re-described from *F. L. Stevens, Fungi of Hawaii 1146*.

In the original description and in Ann. Myc. **26**, p. 170, 1928, Stevens mentions perithecial setae, but all those found near the perithecia in the present specimen arise either from the mycelial hyphae or from the basal perithecial disc.

[Family 222. Sapotaceae.]

133. **Amazonia Sideroxyli** Hansf., sp. n.

Plagulae epiphyllae, atrae, densae, orbiculares, usque ad 2 mm. diam., dispersae, leves. *Mycelium* ex hyphis atrobrunneis, 6–7 μ crassis (cellulis plerumque 15–20 μ longis), subrectis vel leniter flexuosis, opposite ramosis (45–90°), dense reticulato-intertextis compositum, in centro subsolidum. *Hyphopodia capitata* alternata, antrorsa, recta vel curvata, 12–17 μ longa, cellula basali cylindracea vel cuneata, 3–6 μ longa, cellula apicali cylindraceo-clavata, integra, apice late rotundata, recta vel curvula, 9–12 × 7–9 μ. *Hyphopodia mucronata* pauca, dispersa, alternata, ampullacea, curvata, 18–23 × 7–8 μ, collo elongato 3–4 μ cr. *Setae* nullae. *Perithecia* dense stipata, orbicularia, atra, hemispherica vel depresso-globosa, levia, usque ad 300 μ diam., circa 80 μ alt., sursum hyphis radiantibus velata, hyphis ex margine in fimbrias hyphopodiatas productis. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 37–44 × 17–21 μ.

Hab. in foliis *Sideroxyli* spec., Mt. Maquiling, Los Banos, Luzon, Philippine Is., in consortio *Asterinae laxiusculae* Syd., in *Baker, Fungi malay. 509* distributae. (Typus in Herb. Pretoria.)

134. ?Irenina fidelis Toro in Ann. Myc. **32**, p. 112, 1934.

On *Symplocos* sp., Sorsogon, Luzon, Philippine Is., July 1915, *Ramos* (*Philipp. Bur. Sci. 23727 p.p.*, amongst colonies of *Asterina grammocarpa* Syd.).

Only a few colonies were found, and no spores ; the mycelial characters are close to those of *I. fidelis*.

[Family 235. Caprifoliaceae.]

135. **Irenina Linocieriae** (Syd.) Hansf., comb. n.

Syn. *Meliola Linocieriae* Syd. in Ann. Myc. **12**, p. 550, 1914.

Plagulae amphigenae, tenues, orbiculares, usque ad 10 mm. diam., leves. *Mycelium* ex hyphis atrobrunneis, subrectis, 5–6 μ crassis (cellulis plerumque 30–40 μ longis), opposite ramosis (45–60°), laxe reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, 16–22 μ longa, cellula basali cylindracea, 5–10 μ longa, cellula apicali ovata vel clavulato-cylindracea, integra, apice rotundata, 11–16 × 7–9 μ. *Hyphopodia mucronata* alternata, opposita vel inter hyphopodia capitata dispersa, ampullacea, 15–19 × 6–8 μ, collo brevi 3–4 μ crasso. *Setae myceliales* nullae. *Perithecia* dispersa, atra,

globosa, usque ad 150 μ diam., cellulis parietis obtuse conoideis, vix prominulis. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque late rotundatae, 4-septatae, constrictae, 31–38 × 14–16 μ.

Hab. in foliis *Linocieriae cumingianae*, Rizal, Philippines, *Sydow, Fungi exot. exs. 375*, part of type collection ; *Philipp. Bur. Sci., 254.*

In these specimens this species is mixed with the following, and often the two mycelia are interwoven ; in his original description of *Meliola Linocieriae*, Sydow gave the mycelium, perithecia and spores of the present species, but added the setae of the following.

136. **Meliola linocieriicola** Hansf., sp. n.

Plagulae amphigenae, plerumque epiphyllae, densae, atrae, usque ad 4 mm. diam., velutinae. *Mycelium* ex hyphis atrobrunneis, subrectis, 7–8 μ crassis (cellulis plerumque 20–30 μ longis), opposite ramosis (60°), dense reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, 17–24 μ longa, cellula basali cylindracea, 3–5 μ longa, cellula apicali cylindracea vel anguste ovata, apice plerumque subacute rotundata, recta vel curvula, 12–18 × 6–8 μ. *Hyphopodia mucronata* dispersa, opposita vel alternata, ampullacea, 20–25 × 6–9 μ, collo elongato, curvato, 3–4 μ crasso. *Setae mycelia-les* numerosae, dispersae, erectae, atrae, opacae, simplices, rectae, acutae, usque ad 400 × 7–10 μ. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 180 μ diam. *Sporae* atrobrunneae, late ellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 38–45 × 20–21 μ.

Hab. in foliis *Linocieriae Cumingianae* Rizal, Luzon, Philippine Is., *Sydow, Fungi exot. exs. 375 p.p.*, leg. M. Ramos, 14. viii. 1915, in consortio *Ireninae Linocieriae*, sub *Meliola* in *Sydow, Fungi exot. exs. 375*, distributae. (Typus in Herb. Pretoria.)

This is easily distinguished from the preceding species by its closer reticulation, slightly wider hyphae and its rather longer hyphopodia with sharper tips.

[Family 230. Apocynaceae.]

137. **Meliola Forsteroniae** (Stev.) Hansf., comb. n.

Syn. *Meliola Tabernaemontanae* Speg. var. *Forsteroniae* Stevens, in Ill. Biol. Monogr. **2**, p. 50, 1916.

Plagulae amphigenae, atrae orbiculares ver irregulares, 1–2 mm. diam., densae, velutinae. *Mycelium* ex hyphis atrobrunneis, subrectis vel flexuosis, 7–8 μ crassis (cellulis plerumque circa 15 μ longis), opposite ramosis (45–90°), densissime reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, recta vel curvata, 20–32 μ longa, cellula basali late cylindraceo-cuneata, 5–12 μ longa, cellula apicali ovata integraque, vel clavata irregulariterque angulosa vel sublobata, apice rotundata vel truncata, 13–21 × 10–15 μ. *Hyphopodia mucronata* in hyphis distinctis evoluta, alternata vel raro opposita, ampullacea, curvata, 15–20 × 7–9 μ, collo brevi 4–5 μ cr. *Setae myceliales* numerosae, dispersae, erectae, atrae, rectae vel leniter flexuosae, simplices, acutae vel obtusae, usque ad 900 × 10–11 μ. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 160 μ diam. *Sporae* atrobrunneae, crasse cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 37–46 × 18–21 μ [average :] 40 × 20 μ.

Hab. in foliis *Forsteroniae corymbosae*, San Domingo, *Ciferri Micofl. Doming. exs. 153.*

Stevens described this form as *M. Tabernaemontanae* Speg. var. *Forsteroniae*, Ill. Biol.Monogr. **2**, p. 50, 1916, from his own collection (no. 4682) on *F. corymbosa*, Porto Rico ; the irregular hyphopodia and general characters of the mycelium remove it from *M. Tabernaemontanae.*

[Family 232. Rubiaceae!]

138. Amazonia Psychotriae (P. Henn.) Theiss. in Ann. Myc. **11**, p. 499, 1913.

The Herb. Pretoria specimen of *Ciferri, Micofl. Doming. exs. 61*, sub. *Meliola glabra* Berk. et Curt., belongs to this species.

Colonies amphigenous, black, smooth, up to 3 mm. diam. or numerous and confluent over the leaf. Mycelium of dark brown undulate hyphae 7 μ thick, the cells mostly 15–20 μ long, branching usually alternate or irregular at 45–90°, loosely reticulate but becoming dense in the centre of mature colonies. Capitate hyphopodia alternate only, somewhat antrorse, usually straight, 11–16 μ long; stalk cell cuneate to cylindric, 2–8 μ long; head cell globose to broadly ovate, 9–11 μ diam. Mucronate hyphopodia scattered amongst the capitate, bent ampulliform, opposite or alternate, sometimes conoid, 15–18 $\times$ 6–8 μ, with short neck 4–5 μ thick. Setae none. Perithecia closely scattered in centre of colony, flattened to hemispheric with radiate upper wall extending outwards up to 300 μ diam., about 120 μ high, smooth, irregularly dehiscent in centre. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 29–35 $\times$ 12–14 μ.

This specimen has been compared with *Ule 3152* on *Psychotria* sp., Manaos, Amazon, also in Herb. Pretoria, and which appears to be part of the type collection. The spores in this measure 30–35 $\times$ 12–14 μ; Hennings gave them up to 38 μ long, but these large spores probably belong to the *Meliola* sp., probably *M. Psychotriae* Earle, with which the *Amazonia* occurs in mixed infection.

139. **Meliola Erithalidis** (Ciferri) Hansf., comb. n.

Syn. *Meliola Kaduae* Stev. var. *Erithalidis* Ciferri in Ann. Myc. **29**, p. 288, 1931.

—I have compared *Ciferri, Micofl. Doming. exs. 81*, part of the type collection of var. *Erithalidis* Cif., with *F. L. Stevens, Fungi of Hawaii 601*, part of the type of *M. Kaduae*, and find no strong resemblance between them, whereas the differences are so marked as to necessitate the removal of Ciferri's collection from *M. Kaduae* altogether. The San Domingo specimen belongs to a group of species ranging around *M. Psychotriae* Earle as a more or less central type; the differences amongst these species are rather difficult to describe, though comparison under the microscope indicates that for the present it is best to keep them separate, pending the detailed examination of a larger series of collections which may show more intermediate forms.

Colonies amphigenous, black, dense, minute, up to 1 mm. diam., smooth, scattered. Mycelium of dark brown flexuous hyphae 6–7 μ thick, the cells mostly 20–25 μ long, branching opposite or irregular at 45–90°, closely reticulate. Capitate hyphopodia alternate only, more or less antrorse, usually straight, 15–28 μ long; stalk cell cuneate to cylindric, 5–10 μ long; head cell ovate to slightly and irregularly rounded-triangular, rounded at the apex, 12–18 $\times$ 7–11 μ. Mucronate hyphopodia on separate hyphae, alternate ampulliform, more or less bent 13–20 $\times$ 6–8 μ, neck short, 3–4 μ thick. Mycelial setae scattered erect, straight or flexuous, not uncinate, simple acute, up to 400 $\times$ 7–9 μ. No mature perithecia were found in the Pretoria material. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 33–39 $\times$ 13–15 μ. On leaves of *Erithalis parviflora*, San Domingo.

[Family 238. Compositae.]

140. Irene sororcula (Speg.) Stevens in Ann. Myc. **25**, p. 423, 1927.

The following specimens in Herb. Pretoria belong to this species: *F. L. Stevens 8055* on *Eupatorium odoratum*, Porto Rico; *Sydow, Fung. exot. exs. 627* on *E. Oerstedianum*, Costa Rica; *Sydow, Fung. exot. exs. 793* on *Eupatorium*

odoratum, Venezuela ; *Ule, Mycoth. brasil. 73* on an unknown composite, Brazil ; (given by P. Hennings in Hedwigia, **31**, p. 108, 1892 as *Meliola inermis*) ; *Rabh.-Wint., Fungi europ. 3543* appears to be part of the same collection by Ule ; *Ciferri, Micofl. Doming. exs. 150* on *Eupatorium odoratum* ; *F. L. Stevens 7320* on *E. portoricensis*, Porto Rico. IMI. 6043 & 6044

141. IRENINA CYCLOPODA (Stev.) Stevens in Ann. Myc. **25**, p. 452, 1927.

On *Bidens squarrosa*, Costa Rica, *Sydow, Fung. exot. exs. 626* ; on *Pseudelephantopus spicatus*, Porto Rico, *F. L. Stevens 7871*.

[Family 249. Boraginaceae.]

142. IRENINA LONGIPODA (Gaill.) Stevens in Ann. Myc. **25**, p. 459, 1927.

Of specimens assigned to this species I have seen only *Stevens 9239* on *Cordia nitida*, Porto Rico : in this the capitate hyphopodia are regularly alternate antrorse, usually straight, 17–24 μ long, the stalk cell cuneate-cylindric, 4–7 μ long, and the head cell entire ovate, somewhat pointed at the apex, 12–18 × 9–12 μ. These characters are different from those of *Sydow, Fungi exot. exs. 801*, on *Cordia heterophylla*, Venezuela ; Sydow refers his collection to *Meliola Usteriana* Rehm, though Stevens considers this a synonym of *Irenina longipoda*. Sydow's material has the capitate hyphopodia alternate at wide angles or slightly antrorse, straight, 12–18 μ long, the stalk 6–10 μ long and the head cell broadly-ovate to globose, widely rounded at the apex, 10–12 × 10–12 μ. If these specimens are correctly assigned to their respective species above, then it is evident that Stevens' synonomy is incorrect, and that the two species must be retained as distinct.

[Family 250. Solanaceae.]

143. MELIOLA SOLANI Stevens in Illin. Biol. Monogr. **2**, p. 15, 1916.

Syn. *Irenopsis Solani* (Stev.) Stevens in Ann. Myc. **25**, p. 439, 1927.

I have examined *F. L. Stevens 5750*, on *Solanum jamaicense*, Porto Rico, part of the type collection, in Herb. Pretoria, and find that the setae are all mycelial in nature, arising in groups of 8–10 from the hyphae around the base of the perithecium, which form the ' perithecial disc '. Stevens's transfer of this species to his genus *Irenopsis* was therefore incorrect.

144. IRENINA SOLANICOLA (P. Henn.) Stevens in Ann. Myc. **25**, p. 453, 1927.

On *Physalis peruviana*, Hawaii, *F. L. Stevens, Fungi of Hawaii 915* :—

Colonies amphigenous, mostly epiphyllous, dense, black, smooth, up to 1 mm. diam., or confluent and larger. Mycelium of crooked to sinuous dark brown hyphae 6–7 μ thick, the cells mostly 15–20 μ long, the branching close, usually alternate or irregular, closely reticulate and in places almost solid. Capitate hyphopodia alternate (less than 1% opposite) more or less closely antrorse, straight, 13-17 μ long ; stalk cell cylindric to cuneate, 3–6 μ long ; head cell entire globose, 9–11 μ diam. Mucronate hyphopodia usually on separate hyphae, opposite alternate or ternate, closely crowded, ampulliform with long neck 3 μ thick, 14–19 × 5–7 μ. Mycelial setae none. Perithecia closely crowded in centre of colony, black, globose, up to 230 μ diam. ; the surface cells conoid up to 50 μ high by 30–40 μ diam. at the base, tips very bluntly rounded, straight. Spores dark brown cylindric with rounded ends, 4-septate, constricted, 28–33 × 11–12 μ.

I have compared this with South African specimens of *Meliola inermis* K. & C., with which it was identified by Stevens ; the differences are very marked, and the present specimen cannot be retained under that species, though the determination as *I. solanicola* is given with much hesitation, as I have not

yet seen authentic specimens of this species, which was originally described on *Solanum Englerianum* in Tanganyika. Hennings described his species as having globose capitate hyphopodia, but gives the perithecia as smooth and 120–180 μ diam.; the latter characters certainly do not apply in the present instance, where the large conical perithecial cells show a transition towards the 'larviform appendages' of *Irene*. It may eventually prove necessary to erect a new species for the Hawaiian collection on *Physalis*.

[Family 252. Scrophulariaceae.]

145. **Meliola Ulei** Hansf., sp. n.

Plagulae plerumque epiphyllae, raro hypophyllae vel caulicolae, atrae, orbiculares, tenues, usque ad 0·5 mm. diam. *Mycelium* ex hyphis atrobrunneis, undulatis, 5–6 μ crassis (cellulis plerumque circa 15 μ longis), opposite vel irregulariter ramosis (60–90°), reticulatis compositum. *Hyphopodia capitata* alternata (rarissime etiam opposita), leniter antrorsa, recta, 9–13 μ longa, cellula basali cylindracea, 2–4 μ longa, cellula apicali globosa vel late ovata, 7–10 × 7–9 μ. *Hyphopodia mucronata* dispersa, ampullacea, curvata, opposita vel alternata, 12–15 × 5–6 μ, collo brevi 3 μ cr. praedita. *Setae myceliales* haud numerosae, dispersae, erectae, rectae, simplices, obtusae, usque ad 180 × 6 μ. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 130 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 23–29 × 9–10 μ.

Hab. in foliis *Scrophulacearum* spec. indet., Rio Negro, Amazonas, Brazil, *Ule, Mycoth. brasil. 61*, sub *Meliola microspora* Pat. et Gaill. (Typus in Herb. Pretoria.)

This species is rather close to *M. microspora* Pat. & Gaill., of which the type specimen badly needs re-examination to collate it with more recent collections on Labiatae and related host families; its type host was given as 'probably a Labiate', and since 1900 there has been a tendency to refer most small spored collections of *Meliola* on Labiatae to this species.

[Family 257. Bignoniaceae.]

146. **Irenina Schlegeliae** (Stev.) Hansf., comb. n.

Syn. *Irenina glabroides* (Stev.) Stev. var. *Schlegeliae* (Stev.) Stev. in Ann. Myc. **25**, p. 464, 1927.

Meliola glabroides Stev. var. *Schlegeliae* Stev. in Illin. Biol. Monogr. **2**, p. 20, 1916.

F. L. Stevens 8289 on *Schlegelia* sp., Porto Rico, in Herb. Pretoria shows marked differences from specimens of *I. glabroides*:—

Colonies amphigenous, thin, black, smooth, usually effuse and confluent over the whole leaf on both surfaces. Mycelium of dark brown substraight hyphae 6–7 μ thick, the cells mostly 30–50 μ long, branching opposite, alternate or irregular at 30–60°, very loosely reticulate. Capitate hyphopodia alternate only, or more distant, at wide angles straight or bent, 19–30 μ long; stalk cell cuneate to cylindric, straight or bent, 7–11 μ long; head cell irregularly rounded-angulose to shallowly lobate, straight or irregularly bent, 13–21 × 10–20 μ. Mucronate hyphopodia on separate hyphae, alternate or opposite, bent ampulliform with rather long neck 3–4 μ thick, 15–23 × 6–9 μ. Mycelial setae none. Perithecia loosely scattered, black globose verrucose, up to 170 μ diam.; surface cells very bluntly conoid, up to 28 μ high by about 40 μ diam. at the base. Spores dark brown, cylindric to ellipsoid with rounded ends, 4-septate, constricted, 38–46 × 16–20 μ.

147. **Meliola Distictidis** Hansf., sp. n.

Plagulae amphigenae, plerumque epiphyllae, atrae, densae, orbiculares, usque ad 3 mm. diam., dense velutinae. *Mycelium* ex hyphis subrectis, atro-

brunneis, 6–7 μ crassis (cellulis plerumque 30–40 μ longis), opposite ramosis (30–60°), dense reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, recta, 22–30 μ longa, cellula basali cuneata vel cylindracea, 6–13 μ longa, cellula apicali raro subglobosa, plerumque cylindracea vel ovata, apice rotundata vel truncata, margine undulata, crenulata vel irregulariter rotundato-angulosa, 12–20×11–15 μ. *Hyphopodia mucronata* in hyphis distinctis paucis evoluta, plerumque opposita, ampullacea, plus minusve curvata, 20–28×6–9 μ, collo elongato 3–4 μ cr. praedita. *Setae myceliales* numerosae, dense dispersae, erectae, atrae, rectae, usque ad 260×6–9 μ, apice saepe 3-dichotomeo-divisae, ramis patentibus, primariis –15 μ, secundariis –30 μ, tertiariis –15 μ longis, acutae. *Perithecia* dense dispersa, atra globosa verrucosa, usque ad 170 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 36–41×15–16 μ.

Hab. in foliis *Distictidis lactiflorae*, San Domingo, *Ciferri Micofl. doming. exs. 48*, sub *Meliola bidentata* Cooke. (Typus in Herb. Pretoria.)

This was originally determined by Ciferri as *Meliola bidentata* Cooke, from which it is markedly different.

148. Meliola bignoniacearum Stevens in Ann. Myc. **26**, p. 196, 1928.

This is represented in Herb. Pretoria by *Sydow, Fungi exot. exs. 790*, on *Plenotoma diversifolia*, Venezuela. From this, the specimen *Ciferri, Micoflora doming. exs. 48a*, originally determined as *M. bidentata* Cooke, differs in its thinner colonies, narrower hyphopodia and rather different setae, and is best described as a new variety :—

Meliola bignoniacearum Stevens, var. **Tabebuiae** Hansf.

Plagulae epiphyllae, atrae, tenues, usque ad 3 mm. diam., vel in confluendo majores, sparse setosae. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter undulatis, 5–7 μ crassis (cellulis plerumque 20–30 μ longis), opposite ramosis (45–90°), laxe reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, plerumque recta, 13–19 μ longa, cellula basali cylindracea, 3–6 μ longa, cellula apicali anguste ovata vel cylindracea, apice rotundata, integra, 9–16×6–8 μ. *Hyphopodia mucronata* in centro plagularum pauca, opposita vel alternata, plerumque in hyphis distinctis evoluta, ampullacea vel conoidea, 15–18×5–8 μ, collo brevi 3–5 μ cr. praedita. *Setae myceliales* sparsae, erectae, atrae, rectae, usque ad 250×6–7 μ, apice 2–6-dentatae (–7 μ), dentibus plerumque brevissimis, raro apice 2-furcatae (–10 μ). *Perithecia* laxe dispersa, atra, globosa, verrucosa, usque ad 140 μ diam. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 29–35×13–15 μ.

Hab. in foliis *Tabebuiae Berterii*, San Domingo, *Ciferri, Micofl. doming. exs. 48a*, sub *Meliola bidentata* Cooke. (Typus in Herb. Pretoria.)

The setal teeth are often so short as to give the apex a swollen appearance.

149. Meliola bidentata Cooke in Grevillea, **11**, p. 37, 1882.

The following specimens in Herb. Pretoria appear to be assigned correctly to this species : *Rabh.-Wint. Fungi europ. 3546*, on *Bignonia capseolaris*, Green Cove Springs, Florida, leg. Martin ; on *Bignonia capreolata*, Bluffton, S. Carolina, U.S.A., leg. *Mellichamps*, ex. Herb. W. G. Farlow, sub *M. amphitricha* Fr. ; *F. L. Stevens 7347* on *Tecoma pentaphylla*, Porto Rico. In view of the confusion which has existed in regard to this species, I give below a description drawn up from the first of these specimens :—

Colonies epiphyllous orbicular, numerous and confluent, velvety up to 3 mm. diam. when separate, dense. Mycelium of straight dark brown hyphae 6–8 μ thick, the cells mostly 15–25 μ long, branching opposite at 30–45°, closely reticulate and in parts almost solid. Capitate hyphopodia alternate only,

antrorse, usually straight, 20–29 μ long; stalk cell cuneate, 5–8 μ long; head cell entire, ovate, 12–20×9–12 μ. Mucronate hyphopodia few, scattered, opposite or alternate, ampulliform, 15–20×6–8 μ, neck rather short, 2–3 μ thick. Mycelial setae numerous erect straight black simple and acute or 2–3-dentate to 10 μ, up to 340×8–9 μ. Perithecia scattered black globose verrucose, up to 210 μ diam. Spores dark brown, cylindric with rounded ends, 4-septate, constricted, 41–48×15–17 μ.

[Family 263. Verbenaceae.]

150. **Irenina callista** (Rehm) Hansf., comb. n.

Syn. *Meliola callista* Rehm in Leafl. Philipp. Bot. **6**, p. 2191, 1914.

F. L. Stevens in Ann. Myc. **26**, p. 220, 1928, reduces *Meliola callista* Rehm, to synonymy with *M. Callicarpae* Syd. Two specimens of *I. callista* are in Herb. Pretoria: On *Premna odorata*, Los Banos, Laguna, Philippines, *Baker 41*, apparently part of the type collection, and an un-numbered *Baker* specimen on the same host, Mt. Maquiling, Philippines. Both are of the *Irenina* type, without mycelial setae, though the former is parasitized by *Arthrobotryum*, and Rehm may have mistaken the conidiophores of this for mycelial setae. A revised description has been drawn up from *Baker 41*:—

Colonies epiphyllous, black, thin, up to 4 mm. diam. or confluent over the leaf. Mycelium of substraight to slightly flexuous dark brown hyphae 5–7 μ thick, the cells mostly 30–40 μ long, branching opposite or irregular at 45–90°, loosely reticulate. Capitate hyphopodia alternate only, somewhat antrorse or variously bent, 20–30 μ long; stalk cell cuneate to cylindric, often bent, 6–15 μ long; head cell from subglobose and entire to piriform, clavate or somewhat rounded-angulose, straight or bent, 12–16×11–15 μ. Mucronate hyphopodia few, mixed with capitate, ampulliform, more or less bent opposite or alternate, 14–18×7–9 μ, with short neck 4 μ thick. Setae none. Perithecia loosely scattered, black, globose, verrucose, up to 200 μ diam., the surface cells bluntly conical, up to 25 μ high by about 30 μ diam. at the base. Spores dark brown, ellipsoid with rounded ends, 4-septate, constricted, 33–40×14–18 μ.

This is rather close to *Irenina vilis* (Syd.) Stevens on *Callicarpa Blancoi*, Philippines, but the specimens I have so far examined of this species have on the whole rather distinctly smaller and more regular capitate hyphopodia and smaller and smoother perithecia. Whether a further range of collections will necessitate the uniting of these two species must be left to the future to decide. A third species in this group is *Irenina Premnae* Hansford and Deighton (in the press), described from West African collections, having always shorter, regularly globose capitate hyphopodia and rather smaller spores.

151. **Irenina Aegiphilae** Hansf., sp. n.

Plagulae amphigenae, plerumque epiphyllae, 1–5 mm. diam., densae, atrae, leves. *Mycelium* ex hyphis atrobrunneis, flexuosis vel undulatis, 7 μ crassis (cellulis plerumque 25–40 μ longis), alternatim vel opposite ramosis (60–90°), laxe vel dense reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, 19–24 μ longa, cellula basali cylindracea, 4–9 μ longa, cellula apicali clavata vel rotundato-angulosa, saepe leniter irregulari, 10–18×10–15 μ. *Hyphopodia mucronata* alternata vel opposita, dispersa vel saepe in hyphis distinctis evoluta, ampullacea, plus minusve curvata, 15–19×6–8 μ, collo 2–3 μ crasso. *Setae* nullae. *Perithecia* subaggregata, atra, globosa, usque ad 240 μ diam.; cellulis parietis obtuse conoideis vel in processos rectos atrobrunneos usque ad 45 μ alt. et 20 μ diam. elongatis. *Sporae* atrobrunneae, ellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 34–43×13–17 μ.

Hab. in foliis *Aegiphilae alatae*, Valle del Cibao, Prov. Duarte, Rep. Dominicana, *Ciferri, Micofl. Doming. exs. 52*, sub *Meliola Aegiphilae* Stevens. (Typus in Herb. Pretoria.)

This specimen was originally determined by Ciferri as *Meliola Aegiphilae* Stevens, from which it differs in the total absence of setae and in much larger spores.

152. MELIOLA CALLICARPAE Syd. in Ann. Myc. **10**, p. 80, 1912.

Sydow gave the spores of this as 28–32 × 9–11 μ, but the only specimen I have so far seen, *Philipp. Bur. Sci. 27994*, has spores 33–38 × 13–15 μ, with capitate hyphopodia alternate or up to 50 % opposite. From this specimen, *Philipp. Bur. Sci. 25313* on *Premna Cumingiana*, Kalinga, Luzon, P.I., differs in its thinner colonies, in having the capitate hyphopodia almost entirely opposite, the setae rather longer and much less numerous, often grouped around the perithecia, and spores 30–35 × 11–13 μ. It was originally determined as *M. callista* but my observations above indicate that this species belongs to *Irenina*. For the present I include the present specimen under *M. Callicarpae* Syd., together with *Baker, Fung. Malay 43* on the same host, Mt. Maquiling, Los Banos, P.I., which was originally determined by Rehm as *M. cylindrophora* Rehm and still included under that species by Stevens in Ann. Myc. **26**, p. 232, 1928.

153. **Meliola Premnae** Hansf., sp. n.

Plagulae caulicolae, atrae, orbiculares, 1–3 mm. diam. vel confluentes, subdensae. *Mycelium* ex hyphis atrobrunneis, subrectis vel flexuosis, 5–6 μ crassis (cellulis plerumque 20–30 μ longis), opposite vel irregulariter ramosis (30–60 %), in centro plagularum dense reticulatis compositum. *Hyphopodia capitata* alternata, subrecta, plus minusve antrorsa, 16–28 μ longa, cellula basali cylindracea vel cuneata, 6–11 μ longa, cellula apicali subinde breviter lateque subtriangulosa, vel plerumque elongata, ovata integraque, 10–17 × 9–13 μ. *Hyphopodia mucronata* plerumque in hyphis distinctis evoluta, alternata vel opposita curvata, ampullacea, 12–18 × 6–8 μ, collo brevi 3 μ crasso. *Setae myceliales* circum perithecia laxe aggregatae, erectae, flexuosae vel laxe tortae, haud uncinatae, simplices, obtusae, atrae, usque ad 150 × 7–8 μ. *Perithecia* laxe aggregata, atra, globosa, verrucosa, usque ad 150 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 28–34 × 10–12 μ.

Hab. in caulibus *Premnae odoratae*, Philippine Is., *Baker 41* (supplement), sub *Meliola callista* Rehm. (Typus in Herb. Pretoria.)

This is distinguished easily by the flexuous to loosely twisted setae. The hyphopodia are considerably larger than those of *M. micromera* Syd., and much more elongate than those of *M. rizalensis* Syd. What I consider to be the same species occurs in *Philipp. Bur. Sci. 23889* on *Premna nauseosa*, Rizal, Luzon, P.I., but here the hyphopodia are slightly shorter and vary from subglobose to ovate, entire. In this material are large numbers of spores belonging to some foreign *Meliola*, longer and wider and more ellipsoid than those of *M. Premnae*.

[Family 264. Labiatae.]

154. IRENINA ANASTOMOSANS (Wint.) Stevens in Ann. Myc. **25**, p. 456, 1927.

Theissen and Sydow in Ann. Myc. **15**, 461, 1917, agree with Stevens in that this species has no mycelial setae. The specimen in Herb. Pretoria of *Rabh.-Wint., Fungi europaei 3847*, on a Labiate, Minas Geraes, Brazil, leg. *Ule*, has scattered mycelial setae, simple acute, up to 320 μ long, and therefore must be removed from the above species. It is very close to *Meliola microspora* as this species is known from recent collections, but differs in having acute instead of obtuse setae. There is a doubt as to the correct host of the type collection of *M. microspora* Pat. & Gaill., and in any case this needs re-examination to determine whether the more recent collections on Labiatae are correctly referred to it. For the present, to avoid undue multiplicity of species, I include the present

specimen in *M. microspora*, pending a complete revision of the species on Labiatae and nearly related host families.

[Family 11. Lauraceae.]

155. **Meliola Phoebes** Hansf., sp. n.

Plagulae epiphyllae, atrae, leves, tenues, usque ad 10 mm. diam. *Mycelium* ex hyphis atrobrunneis, subrectis, 6–7 μ crassis (cellulis plerumque circa 30 μ longis), opposite ramosis (60–90°), laxe reticulatis compositum. *Hyphopodia capitata* alternata, recta vel curvata, 17–30 μ longa, cellula basali cylindracea, 4–8 μ longa, cellula apicali cylindracea, apice rotundata (subinde subovata), recta vel curvata, 13–25 × 7–10 μ, integra. *Hyphopodia mucronata* dispersa, conoidea vel ampullacea, opposita vel alternata, 15–22 × 7–10 μ, collo brevi, 3–4 μ cr. praedita. *Setae myceliales* paucae, circum perithecia laxe aggregatae, rectae vel subflexuosae, simplices, obtusae, usque ad 450 × 7–9 μ. *Perithecia* laxe dispersa, globosa, atra, verrucosa, matura non visa. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 38–45 × 15–17 μ.

Hab. in foliis *Phoebes costaricanae* in consortio *Asterinae Phoebes* Syd. in *Sydow, Fungi costaric. 167a* distributae. (Typus in Herb. Pretoria.)

The mycelium is rather variable in character in different parts of the same colony, some are straight as described above, while other hyphae are tortuous, up to 10 μ thick and bear shorter and wider hyphopodia.

[Family 319. Velloziaceae.]

156. **Irenina Barbacenniae** Hansf., sp. n.

Plagulae amphigenae, atrae, densae, subcrustosae, leves, usque ad 2 mm. diam. *Mycelium* ex hyphis atrobrunneis, aliis transversis flexuosis, aliis longitudinalibus subrectis, 7–9 μ crassis (cellulis plerumque 15-20 μ longis), opposite vel irregulariter ramosis (45–60°), dense reticulatis compositum, saepe subsolidum. *Hyphopodia capitata* alternata (minus uno per centum opposita), recta vel saepe antrorse curvata, 14–22 μ longa, cellula basali cylindracea, 3–9 μ longa, cellula apicali cylindracea, piriformi integraque, vel irregulari, rotundato-angulosa, versiformi, saepe curvata, 11–18 × 10–15 μ. *Hyphopodia mucronata* pauca, dispersa, alternata vel opposita, ampullacea, 12–17 × 7–9 μ, collo brevi 3–4 μ cr. praedita. *Setae* nullae. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 200 μ diam. *Sporae* atrobrunneae, cylindraceae vel subellipsoideae, utrinque rotundatae, 4-septatae, constrictae, 38–45 × 16–20 μ.

Hab. in foliis *Barbacenniae purpureae*, Rio de Janeiro, Brazil, *Ule*, vi. 1887, *Rabh.-Wint.-Pazschke, Fungi europaei 3849*, sub *Meliola glabra* Berk. et Curt. (Typus in Herb. Pretoria.)

[Family 331. Cyperaceae.]

157. MELIOLA CIRCINANS Earle in Bull. N.Y. Bot. Gard. **3**, p. 304, 1904, emend.

Colonies black, irregular, 5–10 mm. diam., or widely confluent, velvety, easily secedent, rather thin. Mycelium of substraight to flexuous dark brown hyphae 6–7 μ thick, the cells mostly 16–20 μ long, alternately or irregularly branched, loosely to subdensely reticulate. Capitate hyphopodia alternate only, straight or irregularly bent, sometimes more or less uncinate, 15–28 μ long; stalk cell cylindric, 3–9 μ long; head cell usually more or less cylindric, sometimes wider and then somewhat irregularly and shallowly rounded-lobate, straight or more often bent to sinuous, 11–19 × 5–12 μ, typically not more than 8 μ wide. Mucronate hyphopodia rare, scattered, opposite or alternate ampulliform 16–20 × 6 μ. Mycelial setae numerous, scattered, straight, black, simple acute, 400–600 × 8–9 μ. Perithecia scattered, black globose verrucose,

120–150 μ diam., with 6–8 dark brown incurved more or less erect-spreading simple obtuse setae arising from the upper half, up to 130×6 μ. Spores dark brown, cylindric with attenuate-rounded to distinctly apiculate ends, 4-septate, constricted, 30–38×10–13 μ.

The above description is drawn up from one of the two distinct species occurring in *Stevens 5252* on *Scleria* sp., Porto Rico ; the same species occurs also in *Stevens 9221* on *Mariscus jamaicensis*, Porto Rico. The measurements for the spores given above are taken from those actually germinating and thus distinguished from those of other species by the characteristic hyphopodia and narrower mycelium ; it is quite certain therefore that these spores actually belong to this species, in spite of the difference in measurements from those given by Earle (40–45×12 μ), which may refer to those of a second species mixed with *M. circinans*. Earl's type collection needs re-examination to determine this point with certainty.

158. **Meliola apiculata** Hansf., sp. n.

Plagulae epiphyllae, densae, atrae, usque ad 3 mm. diam., subvelutinae. *Mycelium* ex hyphis atrobrunneis, subrectis, undulatis vel flexuosis, 8–9 μ crassis (cellulis plerumque circa 25 μ longis), alternatim vel irregulariter, rarius opposite, ramosis (45–90°), dense reticulatis compositum. *Hyphopodia capitata* alternata, plus minusve antrorsa, recta vel curvata, 20–30 μ longa, cellula basali cylindracea, recta vel curvata, 6–15 μ longa, cellula apicali irregulariter lobata, versiformi, recta vel curvata, 12–22×12–20 μ. *Hyphopodia mucronata* pauca, dispersa, plerumque alternata, anguste ampullacea, 22–26×7–8 μ, collo elongato 3–4 μ cr. praedita. *Setae myceliales* dispersae, erectae, rectae, atrae, rigidae, simplices, acutae, usque ad 1000×10–12 μ. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 180 μ diam., superne setis 4–7, erecto-incurvatis, atrobrunneis, simplicibus, acutis, septatis, usque ad 110×8 μ ornata. *Sporae* atrobrunneae, cylindraceae, utrinque apiculatae, 4-septatae, constrictae, 50–60×17–19 μ.

Hab. in foliis *Scleriae* spec., Porto Rico, in consortio *Meliolae circinantis* Earle in *F. L. Stevens 5252 p.p.* (Typus in Herb. Pretoria.)

As in the last species, the spores above measured were those found germinating on the leaf and producing the characteristic mycelium and hyphopodia, so that there cannot be any doubt that they are correctly assigned to this mycelium. The species occurs mixed with *M. circinans* in the collection, and was originally determined by Stevens as *M. Cyperi*, with the remark that the spores had rounded and not apiculate ends.

159. Meliola argentina Speg. in Anal. Soc, Cient. Argentina, **9**, p. 177, 1880 (Fungi Argent. Pug. I, no. 72.)

In sorting out the following forms I am greatly handicapped in that I have had no access to authentic material of this species. In view of the range of characters shown by these forms with rounded spore ends, the type of this species and that of *M. Cyperi* Pat., which both Spegazzini and Stevens considered to be synonymous, badly require detailed re-examination ; until this is possible I have no option but to describe the following as forms of *M. argentina*, though I am inclined to the view that more than one species is represented.

Form (*a*). On *Rhynchospora corymbosa*, Tunkia, Sierra Leone, *Deighton, M 2203.*

Colonies amphigenous, dense black velvety, up to 5 mm. diam. Mycelium of straight to slightly sinuous or flexuous dark brown hyphae 7–8 μ thick, the cells mostly 20–30 μ long, branching alternate at 45–60°, densely reticulate. Capitate hyphopodia alternate, 23–35 μ long, antrorse ; stalk cell cylindric, 5–11 μ long ; head cell elongate crenate-angulose, rounded to truncate at the

apex, straight or bent, 15–24 × 10–15 μ. Mucronate hyphopodia few, on separate hyphae, alternate or opposite, ampulliform. Mycelial setae numerous, closely scattered, erect, straight, black simple acute, up to 1200 × 10–12 μ. Perithecia scattered black globose verrucose 150–210 μ diam., each with 0–6 curved simple acute black septate setae arising from the sides or the upper half, 80–120 × 6–8 μ. Spores cylindric with rounded ends, 4-septate, dark brown, slightly or scarcely constricted, 50–60 × 15–18 μ.

Form (*b*). On *Mariscus jamaicensis*, San Jose, Laguna, Porto Rico, *F. L. Stevens 9221* (mixed with *M. circinans* Earle);
On *Cladium Mariscus*, San Domingo, *Ciferri, Micofl. doming. exs. 177* (also mixed with *M. circinans*);
On *Cladium jamaicense*, Knysna, Cape Province, S. Africa, Herb, Pretoria 20399;
On *Cyperus flabelliformis*, Bwamba, Uganda, *Hansford 2731* (previously given by me as *M. circinans*).

Colonies epiphyllous, dense black up to 3 mm. diam., moderately setose. Mycelium of substraight dark brown hyphae 7–8 μ thick, the cells mostly 20–30 μ long, branching opposite or irregular at 45–90°, densely reticulate. Capitate hyphopodia alternate, usually strongly antrorse, straight or slightly bent, 18–30 μ long; stalk cell cylindric, 6–13 μ long; head cell very irregularly rounded-lobate, 11–19 × 10–12 μ. Mucronate hyphopodia mostly on separate hyphae, opposite or alternate, ampulliform, more or less bent, 18–23 × 7–9 μ, neck rather long, 3–4 μ thick. Mycelial setae scattered erect black opaque straight simple acute, up to 800 × 10–12 μ. Perithecia scattered black globose verrucose, up to 180 μ diam., with 0–4 erect-spreading simple acute incurved black setae arising from the sides and upper half, up to 120 × 9 μ, usually 3-septate. Spores dark brown cylindric with rounded ends, 4-septate, constricted, 36–42 × 14–15 μ. (Descr. from *F. L. Stevens 9221*.)

The other collections show minor variations around this more or less central type, notably in more flexuous mycelium and setae up to 1110 μ long; the spores vary to some extent: in *Pretoria 20399* 40–47 × 13–17 μ, in *Hansford 2731* 38–42 × 13–15 μ.

Hendrickx 2744 on Cyperaceae indet., Semliki Valley, Congo Belge, is also included here.

Form (*c*). On *Brumea Meyeri*, Olympus, Oahu, Hawaii, *F. L. Stevens, Fungi of Hawaii 711*.

Colonies amphigenous, very dense, black velvety, up to 4 mm. diam. Mycelium of substraight longitudinal hyphae and crooked transverse hyphae, dark brown, 7–9 μ thick, the cells mostly 20–35 μ long, branching opposite or alternate at 30–60 deg., very closely reticulate and almost solid. Capitate hyphopodia alternate, more or less antrorse, usually straight, 18–28 μ long; stalk cell cuneate to cylindric, 5–10 μ long; head cell from subglobose to piriform or oblong, sometimes somewhat irregularly sub-lobed but mostly broadly-rounded at the apex and entire, 13–20 × 11–16 μ. Mucronate hyphopodia rare, ampulliform, mostly alternate, scattered. Mycelial setae scattered erect black opaque straight simple acute, up to 1000 × 9–12 μ. Perithecia scattered black globose verrucose, up to 190 μ diam. Spores dark brown, cylindric with broadly-rounded ends, 4-septate, constricted, 44–51 × 14–15 μ. Perithecial setae 1–6, erect, circinate to merely incurved, simple acute black opaque, 2–3-septate, up to 100 × 7–8 μ, arising from the sides and upper half of the perithecium.

[Family 332. Gramineae.]

160. **Meliola Arundinis** Pat., var. **angulosa** Hansf., var. n.

Plagulae epiphyllae, atrae, densae, velutinae, usque ad 2 mm. diam. *Mycelium* ex hyphis atrobrunneis, subrectis vel tortuosis, 7–10 μ crassis (cellulis

plerumque 15–20 μ longis), opposite vel irregulariter ramosis (45–90°), dense reticulatis compositum, subsolidum. *Hyphopodia capitata* alternata, plus minusve antrorsa, varie curvata, 16–26 μ longa, cellula basali cuneata vel cylindracea, 5–10 μ longa, cellula apicali irregulariter angulosa vel sublobata, 11–18 × 9–17 μ. *Hyphopodia mucronata* dispersa, opposita vel alternata, curvata, ampullacea, 16–24 × 6–9 μ. *Setae myceliales* numerosae, dense dispersae, erectae, rectae, atrae, usque ad 200 μ alt et 10 μ cr., apice 2–3-dichotomeo-divisae, ramis reflexo-patentibus, primariis –20 μ, secondariis –30 μ, tertiariis –15 μ longis, acutis. *Perithecia* dispersa, atra, globosa, verrucosa, usque ad 170 μ diam. *Sporae* atrobrunneae, cylindraceae, utrinque rotundatae, 4-septatae, constrictae, 40–46 × 15–16 μ.

Hab. in foliis *Phragmitis* spec., Philippine Is., *Philipp. Bur. Sci. 9101*, sub *Meliola dichotoma* Berk. et Curt. (Typus in Herb. Pretoria.)

This was originally determined as *M. dichotoma* Berk. and Cooke, the type of which was described on Araliaceae ; it was so recorded by Baker in Leafl. Phil. Bot. **6**, p. 2065, 1914; by Sydow in Philipp. Journ. Sci. **8**, p. 265, 1913, and in Ann. Myc. **15**, p. 165, 1917 ; by Stevens in Ann. Myc. **16**, p. 177, 1928 ; and in Teodoro's Enumeration of Philippine Fungi.

[Family 116. Dipterocarpaceae.]

161. **Asterolibertia Anisopterae** (Sydow) Hansf., comb. n.

Syn. *Asterina Anisopterae* Syd. in Ann. Myc. **12**, p. 556, 1914.
Morenoella Anisopterae Syd. in Ann. Myc. **12**, p. 560, 1914.

Colonies epiphyllous greyish thin, with scattered black thyriothecia, up to 10 mm. diam. or confluent, scarcely visible. Mycelium of dark brown substraight hyphae 6–7 μ thick, the cells mostly 15–20 μ long, branching mostly opposite at about 45–60°, loosely reticulate with polygonal meshes. Hyphopodia intercalary, somewhat darker than the vegetative cells, swollen and often rounded-projecting on one side only, simulating a lateral hyphopodium, outline usually entire, with conspicuous basal pore, 15–20 × 10–15 μ, distributed irregularly along the hyphae though usually the second cell of each branch hypha is so modified. Thyriothecia black, scattered loosely and irregularly, from circular to elliptic or sometimes composite and linear, up to 800 μ long by 300-450 μ wide, convex ; basal wall of subhyaline radiating-longitudinal hyphae 3–4 μ thick, indistinct ; upper wall of dark brown radiating hyphae 4–6 μ thick, the cells up to 15 μ long, the edges loosely fimbriate, the fringing hyphae exhyphopodiate, paler than the mycelium, tortuous-radiating up to 100 μ long ; dehiscence usually by an irregularly longitudinal fissure but with some subsidiary stellate fissures in the shorter and wider thyriothecia ; eventually widely open and exposing the asci. Asci numerous globose aparaphysate, 8-spored, 50–70 × 45–55 μ. Spores dark brown, oblong with rounded ends, 1-septate, constricted, 28–38 × 17–22 μ, the upper cell sometimes slightly larger than the lower, surface very closely and finely punctate. The spores are conglobate in the ascus.

On *Anisoptera thurifera*, Philippines, *Philipp. Bur. Sci. 21908* (type collection of *Asterina Anisopterae* and of the new name *Asterolibertia Anisopterae*) ; *21937* (type collection of *Morenoella Anisopterae*).

162. **Asterolibertia Bakeri** (Sydow) Hansf., comb. n.

Syn. *Asterina Bakeri* Syd. in Ann. Myc. **14**, p. 367, 1916.

Colonies epiphyllous, forming a more or less confluent thin grey-black smooth layer 5–10 mm. diam. Mycelium of substraight dark brown hyphae 3–5 μ thick, with many secondary branches finely sinuous, the cells mostly about 15 μ long, branching usually at 60–90°, loosely reticulate with polygonal meshes. Hyphopodia intercalary, slightly swollen, often arranged regularly

alternate with normal cells, sometimes two together or more scattered, 10–15 × 5–8 μ, barrel-shaped to rarely subglobose, entire, each with small basal pore. Thyriothecia loosely scattered, black convex up to 350 μ diam., usually discrete ; lower wall indistinct ; upper wall of radiating dark brown hyphae 3–5 μ thick, the cells 8–10 μ long ; margin more or less fimbriate, the fringing hyphae tortuous-radiating, often laterally connate into strands or plates, up to 100 μ long, without hyphopodia ; dehiscent by stellate fissures and the central part falling away to expose the asci. Asci numerous ovate thin-walled 8-spored sessile aparaphysate 50–70 × 30–40 μ. Spores conglobate, oblong with rounded ends, dark brown, 1-septate, constricted, 26–36 × 12–14 μ, the cells subequal or the upper slightly larger, epispore very closely verrucose.

Hab. on leaves of *Calamus* sp., Bataan, Luzon, Philippines, *Baker 505, Philipp. Bur. Sci. 23989.*

163, **Asterolibertia Licaniae** (Cooke) Hansf., comb. n.

Syn. *Asterina Licaniae* Cooke in Grevillea, **12**, p. 85, 1884.

Colonies epiphyllous, black, dense, up to 3 mm. diam., smooth. Mycelium of dark brown substraight radiating hyphae 6–9 μ thick, branching close, opposite or irregular, occurring only at the intercalary hyphopodia, closely reticulate and in parts almost solid. Hyphopodia intercalary, more or less alternating with normal cells, somewhat swollen and irregularly barrel-shaped, not darker than normal cells, 7–13 × 9–13 μ, each with a large basal pore. Thyriothecia orbicular, closely scattered, black smooth convex, up to 300 μ diam., or connate and elliptic, up to 450 × 300 μ ; basal wall pale olivaceous, irregularly meandering-radiate ; upper wall of opaque dark brown hyphae radiating outwards, 4–6 μ thick, the cells up to 10 μ long ; margin not usually fimbriate ; breaking irregularly in the centre when mature and soon becoming crateriform by the disintegration and loss of the upper wall. Asci aparaphysate, globose, unripe. Spores widely ellipsoid, smooth subopaque dark brown, 1-septate, constricted, 30–33 × 18–20 μ.

On *Licania* sp., San Francisco, Est. Sta. Catherina, Brazil, *Ule, Rabh.-Wint., Fungi europ. 3746*, sub *Asterina inaequalis* Mont.

Cooke gives the spore measurements as 40–45 × 22–26 μ ; Theissen as 36–40 × 20–26 μ. The spores measured above were all germinating and therefore fully mature.

164. **Asterolibertia licaniicola** Hansf., sp. n.

Plagulae epiphyllae, inter colonias *A. licaniae* commixtae, tenuissimae, oculo nudo haud visibiles. *Mycelium* ex hyphis brunneis, rectis, aliis 4–5 μ crassis, hyphopodiatis (cellulis plerumque 25–30 μ longis), distanter, irregulariter patenterque ramosis, laxissime lateque reticulatis ; aliisque crassioribus, 0–9 μ cr. (cellulis 15–20 μ longis), exhyphopodiatis compositum. *Hyphopodia* irregulariter tenuiterque dispersa, haud regulariter alternata, ramis haud correlata, nonnihil tumida et doliiformia, cellulis typicalibus haud densius colorata, 9–11 × 6–7 μ, poro parvo centrali, basali praedita. *Thyriothecia* irregulariter dispersa, atra, orbiculata, convexa, ad 170 μ diam., margine laxe fimbriata ; hyphis fimbriatis, mycelio pallidioribus, exhyphopodiatis, tortuoso-radiantibus, ad 80 μ longis ; paries superior ex hyphis atrobrunneis, subopacis, 3·5–5 μ crassis (cellulis ad 8 μ longis), in centro stellatim dehiscens. *Asci* non visi. *Sporae* atrobrunneae, oblongae, utrinque rotundatae, 1-septatae, constrictae, leves, 24–28 × 12–15 μ, in germinatione haud collabentes.

Hab. in foliis *Licaniae* sp., San Francisco, Est. Sta. Catherina, Brazil, *Ule*, in socio *Asterinae* in *Rabh.-Wint. Fungi europ. 3746* distributae. (Typus in Herb. Pretoria.)

165. **Asterolibertia nodulosa** (Cooke) Hansf., comb. n.

Syn. *Asterina nodulosa* Speg. in Fung. Puigg. no. 353, in Bol. Acad. Sci. Cordoba, **11**, p. 563, 1889.

Colonies epiphyllous, scattered, orbicular, black, dense, up to 3 mm. diam. Mycelium of straight dark brown hyphae 5–6 μ thick, the cells mostly 20–35 μ long, branching opposite or irregular, loosely reticulate with polygonal meshes. Hyphopodia intercalary, scattered thinly and irregularly along the main hyphae, somewhat swollen and barrel-shaped to subglobose, entire, with conspicuous basal pore, 10–15 × 10–12 μ ; in the more mature parts of the colony the original haustorium formed from each hyphopodium develops into a widely spreading thin more or less circular sheet of pale olivaceous mycelium, extending up to 130 μ diam., and often forming a more or less continuous plate beneath the centre of the colony ; the intramatrical mycelium consists of radiating septate hyphae 2–3 μ thick with cells up to 15 μ long. Thyriothecia closely scattered black convex, orbicular to somewhat elliptic, up to 250 μ diam., or 2–4-connate into irregular ascomata ; basal wall of subhyaline to pale grey radiating hyphae 4–5 μ thick ; upper wall of subopaque dark brown radiating hyphae 5 μ thick, the cells up to 11 μ long ; margin usually loosely fimbriate, the fringing hyphae few, tortuous-radiating, exhyphopodiate, up to 100 μ long. Asci rather few, aparaphysate, sessile or very shortly nodose-stipitate ovate to ellipsoid, 4–8-spored, up to 100 × 50 μ. Spores conglobate, dark brown, oblong-clavulate with rounded ends, 1-septate, constricted, 30–40 × 14–18 μ, closely and rather coarsely black-verrucose.

On *Guatteria dolichopoda*, Costa Rica, *Sydow, Fung. exot. exs. 683.*

The spores on germination produce a short basal hypha which swells up to form an irregularly radiate-lobed dark brown appressorium, at one side of which a hyphopodium develops, forming a haustorium in the leaf. The mycelium grows out from one side of the hyphopodium, which in a few cases seen begins to form a subcuticular plate of mycelium at a very early stage, though in most cases such mycelium develops only at a much later stage in colony development. While the basal cell of the spore is forming the appressorium and hyphopodium, the larger upper cell gradually collapses, followed later by the lower cell ; both soon fall away, and in many film preparations only the appressoria and hyphopodia remain. The appressoria often become muriform by development of septa.

166. **Asterolibertia gibbosa** (Gaill.) Hansf., comb. n.

Syn. *Asterina gibbosa* Gaill. in Bull. Soc. Myc. France, **13**, p. 180, 1897.

Colonies amphigenous, thin, black, up to 1 mm. diam., scattered, orbicular. Mycelium of somewhat undulate to flexuous brown hyphae 5–6 μ thick, the cells mostly 25–30 μ long, branching irregular, rather closely reticulate with rounded-polygonal meshes. Hyphopodia intercalary, slightly swollen, 10–14 × 7–8 μ, each with conspicuous basal pore, entire, scarcely darker than the rest of the mycelium, irregularly scattered along the hyphae. At irregular intervals along the main hyphae and sometimes along the branches, arise subcuticular plates of mycelium, up to about 60 μ diam., one cell deep, formed of radiating hyphae 2–3 μ thick, pale brown in the centre, becoming hyaline towards the periphery ; no specialised cells of the external mycelium are concerned with the origin of these plates. Thyriothecia closely scattered, black convex smooth, up to 90 μ diam. ; basal wall hyaline, indistinctly meandering-radiate ; upper wall of dark brown radiating hyphae 4–6 μ thick, the cells up to 10 μ long ; margin crenate, not fimbriate ; dehiscence by stellate fissures. Asci only unripe in the Herb. Pretoria specimen, aparaphysate, ovate to globose, sessile, 27–32 × 18–24 μ, 4–8-spored (Theissen). Spores conglobate, clavate-oblong with rounded ends, 1-septate, constricted, smooth, brown, 17–21 × 8–9 μ, the upper cell globose and slightly wider than the more elongated lower cell. At germination the lower

cell shrivels up, the contents passing through the upper cell into a short mycelium ending in a hyphopodium; the upper cell then shrivels and little trace remains even in very young colonies of their originating spore. The internal mycelium is formed only in the fairly mature colonies.

On unknown host (? *Randia*, Rubiaceae), Brazil, *Ule, Rabh.-Wint.-Pazschke, Fungi europ. 4054.*

167. **Asterolibertia Ulei** Hansf., sp. n.

Plagulae epiphyllae, orbiculares, atrae, subdensae, leves, dispersae, usque ad 2 mm. diam. *Mycelium* ex hyphis atrobrunneis, rectis, 6–7 μ crassis (cellulis plerumque circa 20 μ longis), opposite ramosis (45–60°), laxe vel subdense polygonaliter reticulatis compositum. *Hyphopodia* intercalaria, sparse dispersa, subglobosa, integra, 8–12 × 9–11 μ, poro conspicuo basali praedita. *Thyriothecia* in centro plagularum dense dispersa, orbiculata, atra, convexa, usque ad 200 μ diam.; paries inferior dilute olivaceus, indistinctus; paries superior ex hyphis radiantibus, subopace atrobrunneis, 4–5 μ crassis (cellulis usque ad 9 μ longis) compositus, margine fimbriatus, hyphis fimbriarum exhyphopodiatis, dilute brunneis, tortuosis, radiantibus, usque ad 70 μ longis. *Asci* aparaphysati, globosi vel ovati, 8-spori, sessiles, immaturi. *Sporae* conglobatae, brunneae, oblongae, utrinque rotundatae, 1-septatae, plus minusve constrictae, 24–30 × 12–17 μ, cellulis subaequalibus, episporio dense subtiliter verruculoso-punctato.

Hab. in foliis Malpighiacearum spec. indet., San Francisco, Santa Catherina, Brazil, Augusto, 1885, *Ule, Rabh.-Wint., Fungi europ. 3437*, sub *Asterina inaequalis* Mont. (Typus in Herb. Pretoria.)

At germination a hyphopodium is formed from the germ tube from the upper cell, while the lower cell collapses; the upper cell shrivels later as the mycelium develops.

168. Asterina Acalyphae Syd. in Ann. Myc. **23**, p. 395, 1925.

Sydow gave the spores as asperulate, but the specimen *Sydow, Fungi exot. exs. 676* in Herb. Pretoria shows them to be smooth or at most very faintly granulose.

169. **Asterina anisoptericola** Hansf., sp. n.

Plagulae hypophyllae, atrae, tenues, leves, usque ad 4 mm. diam. vel late confluentes. *Mycelium* ex hyphis brunneis, flexuosis vel tortuosis, 3–4 μ crassis (cellulis plerumque 20–30 μ longis), dense irregulariterque ramosis, dense reticulatis compositum. *Hyphopodia* laxe irregulariterque dispersa, alternata, 1-septata, cellula basali cylindracea, 2–20 μ longa, cellula apicali irregulariter lobata, 6–14 × 3–7 μ; hyphopodia rarissime continua. *Thyriothecia* laxe dispersa, atra, convexa, orbiculata, usque ad 250 μ diam., vel 2–3-connata et elongata usque ad 700 μ; paries inferior indistinctus, hyalinus; paries superior ex hyphis radiantibus, atrobrunneis, 4–5 μ crassis (cellulis usque ad 10 μ longis), compositus, margine dense fimbriatus; hyphis fimbriarum usque ad 80 μ longis, tortuoso-radiantibus et saepe lateraliter connatis; thyriothecia alia simplicia stellato-dehiscentia, alia composita irregulariter longitudinaliter aperta. *Asci* numerosi, globosi, aparaphysati, 8-spori, sessiles, usque ad 45 μ diam. *Sporae* conglobatae, opace atrobrunneae, leves, 1-septatae, constrictae, cellulis globosis et superiore leniter crassiore, 21–27 × 13–15 μ.

Hab. in foliis *Anisopterae thuriferae*, Rizal, Luzon, Philippine Is., Ramos, viii. 1913, in consortio *Asterinae Anisopterae* Syd. in *Philipp. Bur. Sci. 21908* distributae. (Typus in Herb. Pretoria.)

What may be the *Asterostomella* conidia of this species were found scattered

over the leaf, but were not actually found in pycnidia. There is little differentiation of the hyphopodia from short lateral branches of the mycelium, and some head cells are occasionally found terminal on such branches.

170. ASTERINA ASPERULISPORA Gaill. in Bull. Soc. Myc. France, **13**, p. 180, 1897.

Colonies amphigenous, black, dense, orbicular or confluent and irregular, up to 4 mm. diam., or effuse, especially on the lower surface, smooth. Mycelium of straight (epiphyllous) to crooked (hypophyllous) dark brown hyphae 6 μ thick, the cells mostly 15–20 μ long, branching opposite or irregular at 45–90°, loosely to closely reticulate. Hyphopodia alternate, usually at the distal end of the parent cell, continuous, hemispherical to somewhat elongate, entire, 8–12 × 7–8 μ. Thyriothecia scattered, black, orbicular, convex, up to 130 μ diam. ; lower wall indistinct ; upper wall dark brown, of radiating hyphae 4–7 μ thick, the cells up to 12 μ long ; margin not or only slightly fimbriate ; dehiscence stellate into irregular segments, the centre falling away almost to the margin to expose the asci enclosed by the erect remains of the upper wall. Asci numerous, globose to ovate, 70–80 μ diam., 8-spored, aparaphysate. Spores conglobate, dark brown, oblong with rounded ends, 1-septate, strongly constricted, 38–45 × 20–24 μ, the cells subglobose and the upper slightly wider than the lower ; epispore finely and closely echinulate to about 1 μ. Conidia not found.

On *Ilex* sp., Tubarao, Brazil, *Ule* (re-described from *Rabh.-Wint.-Pazschke, Fungi europ. 4053*, part of the type collection).

171. ASTERINA AUCUBAE P. Henn. in Engl. Bot. Jahrb. **31**, p. 739, 1902.

Specimen : On *Aucuba japonica*, Japan, *Sydow, Fungi exot. exs. 37.*

Colonies black, epiphyllous, dense, up to 5 mm. diam. or confluent over the whole leaf. Mycelium of dark brown substraight hyphae 5–6 μ thick, the cells mostly 20–30 μ long, branching usually opposite at 45–60°, closely reticulate in polygonal meshes. Hyphopodia alternate or unilateral, usually one to each cell at its distal end, continuous, often somewhat antrorse, ovate to sublobate, 8–11 × 5–9 μ. Thyriothecia orbicular, convex, densely crowded to form almost a solid plate, black, mostly discrete but sometimes 2-connate, when single up to 250 μ diam. ; basal wall indistinct, hyaline ; upper wall of dark brown radiating hyphae 4–5 μ thick, the cells up to 10 μ long ; margin closely fimbriate, the fringing hyphae in close parallel strands, tortuous-radiating, exhyphopodiate up to 100 μ long. Asci about 10, globose to ovate, sessile, 8-spored, aparaphysate, 55–90 × 40–50 μ. Spores conglobate, oblong with rounded ends, dark brown, 1-septate, constricted, smooth, 30–38 × 12–14 μ, the upper cell often slightly wider than the lower.

172. ASTERINA CASSIAE Syd. in Philipp. Journ. Sci. **8**, p. 275, 1913.

On *Glochidion llanosii*, Bataan, Luzon, Philippines, *Phil. Bur. Sci. 19012*, and *Sydow, Fungi exot. exs. 135*, parts of the same type collection by P. W. Graff.

Colonies epiphyllous, black, 0·5–1 mm. diam., rather thin, numerous, and confluent often over the whole leaf, smooth. Mycelium of brown hyphae, substraight to somewhat flexuous, 3–4 μ thick, the cells mostly about 20 μ long, branching opposite or irregular at about 60°, loosely to rather closely reticulate with polygonal meshes. Hyphopodia alternate or unilateral, rarely opposite, sessile, at wide angles, cylindric to somewhat irregularly sublobate, 9–12 × 4–6 μ. Thyriothecia closely crowded, black, convex orbicular, up to 150 μ diam. ; basal wall of greyish hyaline radiating hyphae ; upper wall of subopaque dark brown radiating hyphae 3-4 μ thick, the cells up to 7 μ long, margin loosely fimbriate, the fringing hyphae tortuous-radiating exhyphopodiate,

up to 50 μ long ; dehiscence by numerous stellate fissures extending to the margin into narrowly triangular segments, with the central parts finally falling away. Asci about 15, aparaphysate, ovate to subglobose, sessile, 8-spored, 25–40 × 22–30 μ ; spores conglobate, oblong with rounded ends, 1-septate, constricted, 14–20 × 8–9 μ, the cells subequal and subglobose ; epispore finely and shortly echinulate. Pycnidia numerous, mixed with and similar to the thyriothecia ; pycnospores continuous, ovate to piriform, dark brown, smooth, without a hyaline band or prominent germ pores, 10–13 × 9–11 μ.

173. Asterina Dictylomae P. Henn. in Hedwigia, **43**, p. 372, 1904.

On *Dictyloma* sp., Yurimaguas, Peru, *Ule*, s.n. in Herb. Pretoria.

Colonies epiphyllous, black, dense, up to 2 mm. diam., usually numerous and subconfluent over the leaflets. Mycelium of dark brown, substraight to flexuous hyphae 4–5·5 μ thick, the cells mostly 20–30 μ long, branching opposite or irregular, closely reticulate with polygonal meshes. Hyphopodia chiefly restricted to the main hyphae, alternate or unilateral, continuous, sessile, 5–9 μ high by 5–8 μ broad, ovate to subcylindric, entire. Thyriothecia closely scattered but usually discrete, black, convex, orbicular, up to 170 μ diam. ; basal wall subhyaline, of indistinctly radiating hyphae ; upper wall of subopaque dark brown radiating hyphae 4 μ thick, the cells up to 8 μ long, the edge loosely fimbriate, the fringing hyphae exhyphopodiate tortuous-radiating and up to 100 μ long ; dehiscence by a few stellate fissures extending to the margin, the central parts falling away and exposing the asci. Asci aparaphysate sessile ovate to ellipsoid, 8-spored, thick-walled, 45–55 × 35–40 μ. Spores conglobate, dark brown, oblong with rounded ends, 1-septate, constricted, 18–26 × 10–12 μ ; epispore closely and finely verrucose ; the upper cell distinctly larger than the lower.

174. Asterina diplopoda Syd. in Ann. Myc. **25**, p. 56, 1927, emend. Hansf.

On *Solanum acerifolium*, Costa Rica, *Sydow, Fungi costaric. 51* (part of the type collection). On *Solanum callicarpaefolium*, Venezuela, *Sydow, Fungi exot. exs. 846* and *Fungi venezuel. 199*.

In all these collections the *Asterina* is mixed with *Schiffnerula costaricensis* Hansf., described below, and the two mycelia were mixed in Sydow's original description, which also included the spores of the *Schiffnerula* instead of those of the *Asterina*. An emended description is therefore given :—

Colonies mostly epiphyllous, rarely also epiphyllous, scattered loosely over the leaf and mixed with *Schiffnerula costaricensis*, thin, scarcely visible, orbicular, 1–2 mm. diam., smooth. Mycelium of crooked brown hyphae 3·5–4·5 μ thick, the cells mostly 15–30 μ long, branching irregular, loosely reticulate with rounded meshes. Hyphopodia alternate or opposite, or thinly scattered, stipitate, more or less bent, 12–25 μ long ; stalk cell cylindric, bent, rarely straight, 4–15 μ long and 4 μ thick ; head cell irregular to sublobate often bent 6–13 × 4–9 μ. Thyriothecia closely scattered, black, convex, orbicular, up to 100 μ diam., often 2–3-connate and elliptic to irregular ; basal wall very thin, pale grey to olivaceous, radiate ; upper wall of subopaque dark brown radiating hyphae 3–5 μ thick, the cells up to 8 μ long ; margin not or slightly fimbriate, the fringing hyphae few, tortuous radiating, up to 40 μ long, exhyphopodiate ; dehiscence by numerous stellate fissures extending to the margin, into narrowly triangular segments. Asci up to about 10, ripening in succession, ovate to subglobose, sessile, aparaphysate, 8-spored, 33–40 × 25–32 μ ; spores conglobate, dark brown, oblong with rounded ends, 1-septate, constricted, 14–18 × 7–9 μ, the cells subglobose, equal or the upper slightly wider than the lower ; epispore distinctly and loosely verruculose-echinulate.

175. Asterina Gmelinae Sacc. in Nuovo Giorn. Bot. ital. **23**, p. 199, 1916.

Syn. *Asterinella Gmelinae* Sacc. in Sylloge Fungorum **24**, p. 485.

Colonies amphigenous, black, dense, scattered, 3–5 mm. diam., smooth, not usually confluent. Mycelium of dark brown crooked hyphae 5–7 μ thick, the cells mostly 25–30 μ long, branching opposite or irregular, closely reticulate-interwoven with wavy-polygonal meshes. Hyphopodia opposite or alternate, suberect, straight or bent, stipitate, 1-septate, 15–20 μ long ; stalk cell cylindric, 3–6 μ long ; head cell cylindric to narrowly ovate with rounded apex, entire, straight or bent, 10–17 × 5–8 μ. Thyriothecia scattered, orbicular, black, convex, up to 280 μ diam., often 2–3-connate into irregular compound ascomata ; basal wall subhyaline, indistinctly radiate ; upper wall of subopaque dark brown radiating hyphae 4–5 μ thick, the cells up to 10 μ long ; margin crenate ; dehiscence by irregularly stellate fissures in the centre, the central parts falling away and leaving the ascoma widely open. Asci ovate to ellipsoid, sessile aparaphysate, 8-spored, 60–80 × 60–70 μ. Spores conglobate, dark brown, clavate-oblong with broadly rounded ends, 1-septate, strongly constricted, 32–36 × 17–19 μ, the upper cell subglobose and distinctly wider than the more elongate lower cell ; epispore finely verruculose.

On *Gmelina* sp., Mt. Maquiling, Los Banos, Philippines, *Baker, Fung. Malay. 205* (part of type collection).

176. Asterina grammocarpa Syd. in Ann. Myc. **12**, p. 557, 1914.

Colonies epiphyllous, orbicular or irregular, up to 2 mm. diam., usually very numerous and confluent over the whole leaf, black, smooth, thin to dense. Mycelium of undulate brown hyphae 3–4 μ thick, the cells mostly 20–30 μ long, branching opposite or irregular, loosely to closely reticulate with rounded-polygonal meshes. Hyphopodia alternate or more thinly scattered, straight or bent, stipitate, 11–16 μ long ; stalk cell cylindric, 3–7 × 3 μ ; head cell straight or curved, clavate to lobate-expanded above, often closely adnate to hypha, 5–9 × 5–8 μ ; hyphopodia typically at distal end of parent cell. Thyriothecia closely scattered, rounded, up to 160 μ diam., sometimes 2-connate, black, convex ; basal wall subhyaline of radiating hyphae 4 μ thick ; upper wall of radiating dark brown hyphae 4 μ thick, the cells up to 8 μ long, margin loosely fimbriate, the fringing hyphae tortuous radiating up to 40 μ long ; dehiscent by numerous stellate fissures. Asci about 10, globose to ovate, aparaphysate, 8-spored, 35–40 μ diam. Spores conglobate, brown, oblong with rounded ends, 1-septate, constricted, 17–22 × 7–9 μ, the upper cell slightly wider than the lower and subglobose ; epispore minutely verrucose, the granules in more or less definite longitudinal lines.

On *Symplocos* sp., Philippines, *Philipp. Bur. Sci. 21834* (part of the type collection), *23727*.

177. Asterina Lawsoniae P. Henn. & P. Nym. in Monsunia **1**, p. 159, 1899.

Specimen : *Sydow, Fung. exot. exs. 137*, on *Lawsonia alba*, India :—

Colonies amphigenous, dense, black, smooth, up to 1 mm. diam., usually very numerous and confluent over the leaf. Mycelium of sinuous brown hyphae 3·5–5 μ thick, the cells mostly 10–15 μ long, branching close, opposite, alternate or irregular, closely reticulate-radiating and towards the centre almost solid. Hyphopodia alternate, at the distal ends of the parent cells, sessile, continuous, pulvinate, expanded and sometimes sublobate above, about 5 μ long and 5–8 μ wide. Thyriothecia closely scattered, black, orbicular, convex, up to 140 μ diam. ; lower wall indistinct, hyaline ; upper wall of radiating dark brown hyphae 3–4 μ thick, the cells up to 7 μ long ; margin scarcely fimbriate ; dehiscent by numerous stellate fissures extending to the margin into narrowly triangular segments, The thyriothecia are often 2–3-connate into compound

ascomata. Asci up to 10, aparaphysate, ovate to ellipsoid, sessile, 8-spored, 28–35 × 25–30 μ. Spores conglobate, oblong with rounded ends, 1-septate, constricted, 17–20 × 7–9 μ, the cells subequal; epispore smooth (not verruculose as given by Sydow). Pycnidia very numerous, similar to the thyriothecia but only about 90 μ diam.; pycnospores oblong to ovate, continuous, dark brown with a central hyaline transverse zone, 14–20 × 7–9 μ.

178. Asterina laxiuscula Syd. in Phil. Journ. Sci. **8**, p. 276, 1912.

On *Sideroxylon ferrugineum*, Philippines, *Sydow, Fung. exot. exs. 269* (part of the type collection).

Colonies epiphyllous, black, rather dense, smooth, orbicular up to 4 mm. diam., usually scattered and not confluent. Mycelium of dark brown substraight hyphae 4·5–5·5 μ thick, the cells mostly 20–30 μ long, branching alternate or opposite at 30–60°, rather closely reticulate with polygonal meshes. Hyphopodia alternate or unilateral, sessile, continuous, hemispheric to shortly cylindric, entire, straight, 6–10 × 5–7 μ. Thyriothecia scattered, black, orbicular, convex, up to 300 μ diam., or 2–3-connate into larger irregular compound ascomata; basal wall greenish hyaline, indistinctly radiate, very thin; upper wall of subopaque dark brown radiating hyphae 3–4·5 μ thick, the cells up to 8 μ long; margin more or less fimbriate, the fringing hyphae radiating, up to 60 μ long, exhyphopodiate; dehiscence by stellate fissures in the central part, the cells falling away to form an irregular large central pore. Asci aparaphysate, embedded in brownish mucus, ovate to ellipsoid, 55-75 × 40–50 μ, 8-spored, sessile. Spores dark brown, oblong with rounded ends, 1-septate, constricted, smooth, 30–34 × 13–15 μ, conglobate in the ascus.

The same species is contained in *Baker 509* (issued in error as 809), Los Banos, Philippine Is.

179. Asterina Litseae Yates in Philipp. Journ. Sci. **13**, p. 373, 1918.

On *Litsea* sp., Burgos, Luzon, P.I., *Philipp. Bur. Sci, 27842*, part of the type collection :—

Colonies amphigenous, mostly epiphyllous, orbicular to irregular, up to 7 mm. diam., usually widely confluent over the leaf, thin, black, smooth. Mycelium of substraight dark brown hyphae 3·5–4·5 μ thick, the cells mostly 25–30 μ long, branching opposite or irregular at wide angles, loosely reticulate with angular, often rectangular meshes. Hyphopodia alternate or opposite, produced usually near the middle of the parent cell, continuous, usually straight, at wide angles, cylindric to obtusely conoid, entire, 6–9 × 4–5 μ. Thyriothecia closely scattered, orbicular, black, convex, up to 120 μ diam., often 2–3-connate into larger irregular compound ascomata; basal wall hyaline, indistinct; upper wall of subopaque dark brown radiating hyphae 3 μ thick, the cells up to 6 μ long; margin more or less fimbriate, the fringing hyphae loosely tortuous-radiating, exhyphopodiate up to 80 μ long; dehiscent by about 6 stellate fissures extending to the margin, exposing the asci enveloped in a yellowish mass of tough mucus. Asci up to 10, ripening in succession, aparaphysate, subglobose to ovate, sessile, 8-spored, 30–35 × 20–25 μ. Spores conglobate, oblong with rounded ends, 1-septate, constricted, dark brown, 15–17 × 8–9 μ, the cells subequal or the upper slightly larger, both subglobose; epispore delicately and closely verruculose.

180. Asterina melanomera Syd. in Ann. Myc. **15**, p. 241, 1917.

On *Dasymaschalon clusiflorum*, Lahuna, Luxon, Philippine Is., *Baker 510* :—

Colonies mostly epiphyllous, black, dense, smooth, 5–10 mm. diam., or widely confluent over the leaf. Mycelium of substraight dark brown hyphae 6–7 μ thick, the cells mostly about 25 μ long, branching alternate or irregular, closely reticulate with polygonal meshes. Hyphopodia scattered along the main

hyphae only, alternate or unilateral, sessile continuous, hemispheric, entire, 9–12 × 10–11 μ. Thyriothecia rather densely scattered, black, convex, orbicular, up to 240 μ diam. ; usually discrete ; lower wall pale olivaceous, indistinctly tortuous-radiate, very thin ; upper wall of subopaque dark brown radiate hyphae 6–7 μ thick, the cells about 10 μ long, margin loosely fimbriate, the fringing hyphae straight, radiating, exhyphopodiate, up to 150 μ long ; dehiscence by irregularly stellate fissures in the central part, which falls away leaving the asci surrounded by the black margin of the thyriothecium. Asci aparaphysate, globose to ovate, sessile, 8-spored, 35–55 × 30–45 μ, spores conglobate, dark brown, oblong with rounded ends, 1-septate, constricted, 25–30 × 12–14 μ, the cells subequal or the upper slightly larger ; epispore densely and distinctly verrucose.

181. **Asterina rizalensis** Hansf., sp. n.

Plagulae epiphyllae, minutae, tenues, aegre perspicuae, usque ad 1 mm, diam., griseae. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter flexuosis, 5–6 μ crassis (cellulis plerumque 25–30 μ longis), opposite vel irregulariter ramosis (45–90°), laxe reticulatis compositum. *Hyphopodia* usque ad 90 %. opposita, continua, obtuse conoidea, saepe sinuoso-curvata et subinde irregulariter sublobata, 11–14 × 5–8 μ. *Thyriothecia* laxe dispersa, atra, convexa, orbiculata, usque ad 240 μ diam. ; paries inferior indistinctus ; paries superior ex hyphis radiantibus opace atrobrunneis, 4–5 μ crassis (cellulis 4–9 μ longis) compositus, margine non vel vix fimbriatus, hyphis fimbriarum paucis, tortuoso-radiantibus, exhyphopodiatis, usque ad 80 μ longis ; thyriothecium in centro irregulariter dehiscens et parte centrali decidente. *Asci* aparaphysati, globosi, sessiles, usque ad 15, 50–60 μ diam. *Sporae* conglobatae, atrobrunneae, oblongae, utrinque rotundatae, 1-septatae, constrictae, 28–32 × 14–17 μ, cellulis subaequalibus vel superiore leniter crassiore, episporio levi.

Hab. in foliis *Anisopterae thuriferae*, Rizal, Luzon, Philippine Is., in consortio *Asterinae Anisopterae* Syd. in *Philipp. Bur. Sci. 21908* distributae. (Typus in Herb. Pretoria, 21937.)

182. Asterina Schmideliae Gaill. in Bull. Soc. Myc. France **13**, p. 181, 1897.

On *Schmidelia* sp., Tubarao, Santa Catherina, Brazil, *Ule 1018* (*Rabh.-Wint.-Pazschke, Fungi europ. 4055*) :—

Colonies epiphyllous, grey-black, orbicular to irregular, 2-3 mm. diam., usually very numerous and confluent over the leaf. Mycelium of substraight to crooked dark brown hyphae 5–6 μ thick, the cells mostly 15–20 μ long, branching opposite or irregular, often rectangular, closely reticulate with polygonal meshes. Hyphopodia alternate or more scattered, sessile, suberect, continuous conical, to cylindric, entire, straight, 7–10 × 6–8 μ. Thyriothecia closely scattered, black, convex, orbicular up to 200 μ diam., usually discrete ; lower wall greyish hyaline, indistinctly radiate ; upper wall of subopaque dark brown radiating hyphae 3–4·5 μ thick, the cells up to 8 μ long ; margin usually fimbriate, the fringing hyphae numerous tortuous-radiating exhyphopodiate, up to 80 μ long, often laterally agglutinate into strands or plates ; dehiscence by stellate fissures extending nearly to the margin, into broadly triangular segments, the central parts falling away and exposing the asci. Asci about 8, ripening in succession, ovate to ellipsoid, sessile, aparaphysate 8-spored, 60–70 × 45–55 μ. Spores conglobate, dark brown, oblong with rounded ends, 1-septate, constricted, 30–34 × 15–18 μ, the upper cell slightly larger than the lower, epispore closely and finely echinulate.

183. ASTERINA TRACHYCARPA Syd. in Leafl. Philippine Bot. **5**, p. 1542, 1912.

On *Derris sinuata*, Singapore, *Baker 401* : included incorrectly by Saccardo in *Asterina singaporensis* Syd.

Colonies epiphyllous, grey-black, very thin, smooth, orbicular, up to 5 mm. diam., scattered thinly over the leaf and sometimes confluent. Mycelium of substraight brown hyphae 3–4 μ thick, the cells mostly 25–30 μ long, branching opposite or irregular at 45–60°, loosely reticulate with polygonal meshes. Hyphopodia opposite or alternate at wide angles, sessile continuous, cylindric to somewhat ampulliform with rounded apex, straight or more or less bent, 9–13 μ long, 3–5 μ broad. Thyriothecia loosely scattered, rounded, black convex, up to 160 μ diam. ; basal wall hyaline indistinct ; upper wall of radiating subopaque dark brown hyphae 3 μ thick, the cells up to 6 μ long, margin loosely fimbriate, the fringing hyphae tortuous-radiating exhyphopodiate and up to 60 μ long ; dehiscence by stellate fissures and the central part falling away leaving the asci inside the crateriform remains of the ascoma. Asci about 8, aparaphysate, globose to ovate, sessile 8-spored, 25–30 diam. Spores conglobate, pale brown, oblong with rounded ends, 1-septate, slightly constricted, smooth, 14–16 × 6–8 μ, the cells subequal. Germination by production of a short hypha with a single pair of hyphopodia, the cells of the spore then shrivelling away before further development of the young colony.

184. **Asterina submegas** (P. Henn.) Hansf., comb. n.

Syn. *Seynesia submegas* P. Henn. in Hedwigia, **43**, p. 374, 1904.

Colonies epiphyllous only, scattered black, rather dense, up to 4 mm. diam. Mycelium of substraight dark brown hyphae 5 μ thick, the cells mostly about 25 μ long, branching opposite or irregular at 45–60°, loosely to rather closely reticulate with polygonal meshes. Hyphopodia alternate or opposite, mostly straight and short cylindric, sometimes slightly irregular to somewhat ampulliform, rounded at the apex, 8–12 × 4–7 μ, at wide angles to the hyphae. Thyriothecia scattered, black, convex, rounded, up to 200 μ diam., sometimes 2-connate ; lower wall of hyaline radiating hyphae about 2 μ thick, indistinct ; upper wall of subopaque dark brown radiating hyphae 4–5 μ thick, the cells up to 10 μ long, margin loosely fimbriate, the fringing hyphae exhyphopodiate, slightly paler than the mycelium, tortuous-radiating up to 120 μ long ; dehiscence by rather numerous stellate fissures into narrowly triangular segments, the central cells falling away and exposing the asci. Asci up to about 10, subglobose to ovate, aparaphysate, 8-spored, sessile. Spores conglobate, dark brown, oblong with rounded ends, 1-septate, strongly constricted, 30–37 × 16–20 μ, the upper cell distinctly wider than the lower ; epispore closely and finely verruculose.

On *Guarea* sp., Jurua, Amazon, *Ule, Mycoth. brasil. 67*.

185. ASTERINA TURNERAE P. Henn. in Hedwigia, **43**, p. 371, 1904.

Colonies amphigenous, black, dense, smooth, up to 3 mm. diam., or confluent and larger. Mycelium of crooked brown hyphae 3–4 μ thick, the cells mostly about 20–25 μ long, branching opposite or irregular, closely reticulate with wavy meshes. Hyphopodia alternate or unilateral, sessile or very shortly stipitate, continuous, expanded and 2–4-lobate above, 5–7 × 6–10 μ Thyriothecia closely scattered, black, convex, rounded, up to 100 μ diam., frequently 2–3-connate-into larger irregular compound ascomata ; basal wall hyaline, indistinct ; upper wall of subopaque dark brown hyphae 3–4 μ thick, the cells up to 7 μ long, margin not fimbriate ; dehiscence by numerous stellate fissures to the margin into narrowly triangular segments, the centre falling away and exposing the asci. Asci about 8, aparaphysate, ovate to subglobose, sessile 8-spored, about 30 μ diam. Spores conglobate, brown, oblong with rounded ends, 1-septate,

constricted, 15–18×9–10 μ, the cells subequal or the upper slightly larger; epispore finely and closely verruculose.

On *Turnera ulmifolia*, Tarapoto, Peru, *Ule, Mycoth. brasil. 66.*

186. **Asterina Champereiae** Hansf., sp. n.

Plagulae epiphyllae, atrae, leves, tenues, orbiculares, usque ad 2 mm. diam., vel numerosae late confluentesque. *Mycelium* ex hyphis atrobrunneis, subrectis vel leniter flexuosis, 3·5–5 μ crassis (cellulis plerumque 15–20 μ longis), opposite vel irregulariter ramosis, subdense reticulatis compositum, maculis retis mycelialis polygonalibus. *Hyphopodia* alternata vel usque ad 30 % opposita, stipitata, suberecta, 10–13 μ longa; cellula basali cylindracea, 2–5 μ longa, cellula apicali cylindracea, anguste ovata vel irregulariter sublobata, 6–9×3·5–5 μ, recta vel curvata. *Pycnidia* dense dispersa sed plerumque discreta, orbiculata, atra, convexa, usque ad 90 μ diam.; paries inferior ex hyphis griseis vel olivaceis, radiantibus, 3–5 μ crassis, indistincte septatis compositus; paries superior ex hyphis atrobrunneis, radiantibus, 4 μ crassis, cellulis usque ad 7 μ longis compositus, margine laxe fimbriatus; hyphis fimbriarum exhyphopodiatis, tortuoso-radiantibus, brunneis, usque ad 40 μ longis; pycnidium stellatim ad marginem dehiscens, demum late apertum. *Pycnosporae* atrobrunneae, late ovatae, basi leniter apiculatae, continuae, leves, 14–16×12–14 μ, zono hyalino et poris germinationis conspicuis nullis. *Thyriothecia* pycnidia consimilia, usque ad 130 μ diam. (immatura); asci et sporae maturae non visae.

Hab. in foliis *Champereiae Cumingianae*, Mt. Maquiling, Los Banos, Luzon, Philippine Is., *Baker 115* sub *Asterina decipiente* Syd. (Typus in Herb. Pretoria.)

This specimen was incorrectly determined as *A. decipiens* Syd., which has continuous hyphopodia and different pycnospores with prominent germ pores.

187. **Stachybotryella bispora** Hansf., sp. n.

Plagulae hypophyllae, inter *Morenoellam Memecyli* Syd. interspersae, tenuissimae, effusae, oculo nudo haud perspicuae. *Mycelium* ex hyphis dilute olivaceis, 2–3 μ crassis, indistincte septatis, irregulariter ramosis, subdense reticulatis, omnino superficialibus, flexuosis compositum, hyphis secondariis subhyalinis vel hyalinis. *Conidiophora* in hyphis mycelii lateralia, erecta, recta, simplicia, dilute olivacea, 1–3-septata, sursum leniter crassiora (0–4 μ), usque ad 60 μ longa. *Conidia* singula, terminalia, ex cellula apicali conidiophori et cellulis duobus lateralibus composita, cellulis lateralibus subglobosis, atrobrunneis, 9–11 μ diam., verrucosis.

Hab. in foliis *Memecyli subfurfuracei*, Bataan, Luzon, Philippine Is., in socio *Morenoellae Memecyli* Syd. in *Philipp. Bur. Sci. 9100* distributae.

This fungus appears to be completely superficial and saprophytic in habit. Though the mycelium is mixed with that of other fungi on the leaves, it does not appear to be parasitic on any of them, and I have been unable to detect any penetration into the host leaf. The conidiophores are loosely scattered along the hyphae, arising from these as erect lateral branches up to 60 μ long; the conidia or bulbils consist of the somewhat swollen apical cell of the conidiophore, bearing two opposite subglobose cells laterally; the latter are dark brown with a thick epispore dotted with paler brown warts, while the apical cell of the conidiophore is paler brown to subhyaline and less prominently verrucose.

188. **Schiffnerula Crotonis** Hansf., sp. n.

Plagulae epiphyllae, inter *Asterinam crotonicolam* Pat., interspersae, griseo-atrae, tenues, leves, usque ad 1 mm. diam. *Mycelium* ex hyphis tortuosis, dilute brunneis, 7–8 μ crassis (cellulis plerumque circa 20 μ longis), dense

irregulariterque ramosis, dense reticulatis compositum. *Hyphopodia* alternata vel unilateralia, hemisphaerica, integra, continua, sessilia, 10–12 μ diam. *Perithecia* dense dispersa, subglobosa, primo atrobrunnea, demum pallidescentia, usque ad 100 μ diam. et circa 50 μ alt., glabra ; paries unistratosus parenchymaticus, in maturitate mucoso-diffluens. *Asci* 2–3, in successione maturescentes, globosi vel ovati, sessiles, aparaphysati, usque ad 45 μ diam., 8-spori. *Sporae* conglobatae, brunneae, oblongae, utrinque rotundatae, 1-septatae, constrictae, leves, 23–28 $\times$ 14–17 μ, cellulis subaequalibus et subglobosis. *Conidia falcata* dilute brunnea, utrinque pallidiora, curvata, fusoidea, 3-septata, non vel vix constricta, apice rotundata, basi subapiculata, 35–42 $\times$ 14–17 μ. *Conidia sarcinelliformia* subglobosa, opace atrobrunnea, muriformia, usque ad 30 μ diam.

Hab. in foliis *Crotonis gossypifolii*, Costa Rica, in consortio *Asterinae crotonicolae* in *Sydow, Fungi exot. exs. 678* distributae. (Typus in Herb. Pretoria.)

The *Sarcinella* conidia or bulbils are present only in some colonies.

189. **Schiffnerula costaricensis** Hansf., sp. n.

Plagulae epiphyllae, minutae, usque ad 0·5 mm. diam., dense dispersae et subinde confluentes, aegre perspicuae, griseo-atrae. *Mycelium* ex hyphis dilute olivaceis, tortuosis, 5–7 μ crassis (cellulis plerumque circa 20 μ longis), irregulariter ramosis, dense reticulatis compositum. *Hyphopodia* alternata vel unilateralia, hemisphaerica, integra, continua, concolorata, 8–11 μ diam. *Conidia falcata* dilute olivacea, utrinque subhyalina, curvato-fusoidea, apice rotundata, basi subapiculata, 3-septata, haud constricta, levia, 22–26 $\times$ 13–14 μ, cellulis centralibus majoribus. *Conidia sarcinelliformia* non visa. *Perithecia* dense dispersa, subglobosa, subhyalina vel dilute lutea, usque ad 60 μ diam. ; paries parenchymaticus unistratosus, in maturitate mucoso-diffluens. *Asci* maturi non visi. *Sporae* dilute olivaceae vel brunneae, oblongae, utrinque rotundatae, 1-septatae, constrictae, leves, 17–21 $\times$ 9–12 μ, cellula superiore saepe leniter crassiore.

Hab. in foliis *Solani laurifolii*, S. Pedro de S. Ramon, Costa Rica, in consortio *Asterinae consobrinae* Syd. in *Sydow, Fungi costaric. 56b* distributae. (Typus in Herb. Pretoria.)

190. **Schiffnerula Periplocae** Hansf., sp. n.

Plagulae epiphyllae, tenues, atrae, usque ad 3 mm. diam., dispersae vel confluentes, leves. *Mycelium* ex hyphis subrectis vel flexuosis, 5–6 μ crassis, brunneis (cellulis plerumque 15–20 μ longis), irregulariter ramosis, dense reticulatis compositum, in centro plagularum subsolidum. *Hyphopodia* alternata vel dispersa, in hyphis primariis evoluta, continua, integra, hemisphaerica vel ovata, 8–10 $\times$ 6–7 μ. *Conidia falcata* brunnea, utrinque pallidiora, curvato-fusoidea, apice rotundata, basi subapiculata, 3-septata, haud constricta, levia, 25–33 $\times$ 9–11 μ. *Conidia sarcinelliformia*, in plagulis aliis numerosa, in aliis pauca, subglobosa, atrobrunnea, levia, muriformia, usque ad 30 μ diam. *Perithecia* dense dispersa, depresso-globosa, brunnea, glabra, usque ad 90 μ diam., interdum connata, circa 40 μ alt. ; paries unistratosus parenchymaticus, in maturitate mucoso-diffluens. *Asci* usque ad 10, in successione maturescentes, aparaphysati, globosi, 25–30 μ diam., 8-spori. *Sporae* conglobatae, oblongae, utrinque rotundatae, 1-septatae, constrictae, leves, dilute brunneae, 13–17 $\times$ 7–8 μ, cellula superiore leniter crassiore.

Hab. in foliis *Periplocae nigrescentis*, Sierra Leone : Tawia, Bake Loko, *Deighton, M 1849.* (Typus.)

This differs from *S. Doidgeae* Hansf. on *Cynanchum* in South Africa, in its larger perithecia containing more asci, and in the considerably smaller spores.

191. SCHIFFNERULA MIRABILIS von Höhnel, Fragm. zur Mykologie, no. 330, 1909.

On *Passiflora quadrangularis*, Sierra Leone, Tengama, Nimi Koro, *Deighton, M 1485* ; Mano, Basse, *Deighton, M 2439.*

These specimens are a close approach to collections on *Passiflora* in Uganda, and differ from the following in darker colonies, closer, straighter hyphae and denser reticulation ; the perithecia are more obviously globose and parenchymatous. For the present all collections are retained in the single species.

On *Passiflora foetida*, Sierra Leone : Mabang, Ribi, *Deighton, M 1023* ; Njala, Kori, *Deighton, M 426* ; Kenema, Nongowa, *Deighton, M 1432* ; Magburaka, *Deighton, M 2422* ; Rokupr, Magbema, *Deighton, M 1555* ; Taiama, Kori, *Deighton, M 1330.*

On *Adenia lobata*, Sierra Leone : Njala, Kori, *Deighton, M 2423.*

192. **Schiffnerula Cassiae** Hansf., sp. n.

Plagulae amphigenae, pallide olivaceae, tenues, usque ad 1 mm. diam. vel subinde confluentes, *Mycelium* ex hyphis dilute griseo-hyalinis, 5 μ crassis (cellulis plerumque circa 20 μ longis), flexuosis, irregulariter ramosis, laxe reticulatis compositum. *Hyphopodia* alternata, hemisphaerica vel leniter elongata, continua, sessilia, integra, 7–9 μ diam. *Conidia falcata* pauca, curvato-fusoidea, apice rotundata, basi subapiculata, 3-septata, non vel vix constricta, hyalina, 30–35 × 9–11 μ. *Conidia sarcinelliformia* subglobosa, opace atrobrunnea, levia, muriformia, usque ad 30 μ diam. *Perithecia* numerosa, in hyphis mycelii lateralia, subglobosa, hyalina vel dilute crocea, levia, glabra, usque ad 70 μ diam. et 50–60 μ alt. ; paries unistratosus parenchymaticus, in maturitate superne mucoso-diffluens. *Asci* 3–6, in successione maturescentes, globosi vel ovati, sessiles, 8-spori, aparaphysati, 30–35 μ diam. *Sporae* conglobatae, oblongae, utrinque rotundatae, 1-septatae, leniter constrictae, leves, 15–18 × 8–9 μ, cellula superiore leniter crassiore, diu hyalinae, postremo dilute olivaceae vel brunneae.

Hab. in foliis *Cassiae Kirkii*, Sierra Leone, Jokibu, Peje West, *Deighton, M 2147.* (Typus.)

The colonies are often almost white, becoming grey-black with the formation of the *Sarcinella* bulbils, or yellowish with formation of perithecia.

193. **Armatella Yatesii** Hansf., sp. n.

Plagulae epiphyllae, atrae, leves, orbiculares, densae, usque ad 5 mm. diam., vel numerosae lateque confluentes. *Mycelium* ex hyphis rectis, atrobrunneis, 6–7 μ crassis (cellulis plerumque 25–30 μ longis), alternatim vel irregulariter ramosis (45–60°), dense reticulatis compositum, *Hyphopodia capitata* alternata, suberecta, plerumque recta, 20–25 μ longa, cellula basali cylindracea, 3–6 μ longa, cellula apicali irregulariter stellato-lobata, 12–18 × 11–17 μ. *Hyphopodia mucronata* nulla. *Setae* nullae. *Perithecia* subglobosa, dispersa, atra, verrucosa, usque ad 220 μ diam., in subiculo radiato denso efformata, hyphis subiculi usque ad 80 μ longis, exhyphopodiatis. *Sporae* brunneae, translucentes, oblongae, utrinque rotundatae, 1-septatae, non vel vix constrictae, 35–48 × 12–14 μ, episporio tenui, sparse indistincteque verruculoso.

Hab. in foliis *Neolitseae* spec., Philippine Is. ; Mt. Posuey, Prov. Abra, Luzon, *Philipp. Bur. Sci. 27083*, sub *Asterina Neolitseae* Yates, leg. *Ramos.* (Typus in Herb. Pretoria.)

Under the microscope this is obviously different from the type of *Armatella Litseae* Syd., in its stouter hyphae and considerably larger hyphopodia, which usually have the terminal lobe much larger than the others. I was unable to find any trace of roughness on the spores taken from *Philipp. Bur. Sci. 27076*, which is *A. Litseae* Syd. In both species the spores germinate by production of a hyphopodium from one of the two cells, the other cell rapidly collapsing.

194. **Lembosia fallaciosa** (Sydow) Hansf., comb. n.

Syn. *Asterina fallaciosa* Syd. in Ann. Myc. **15**, p. 240, 1917.

On *Canarium* sp., Laguna, Luzon, Philippine Is., *Philipp. Bur. Sci. 23774.* (Type collection) :—

Colonies epiphyllous, orbicular, 3–5 mm. diam., or larger and confluent over the leaf, black, thin, smooth. Mycelium of substraight to slightly flexuous dark brown hyphae 6–7 μ thick, the cells mostly 20–30 μ long, branching usually opposite at 45–60°, rather closely reticulate with polygonal meshes. Hyphopodia numerous, opposite alternate or ternate, at wide angles, irregularly cylindric to somewhat ampulliform, with more or less sinuous outline and often bent at the rounded apex, continuous, sessile, 12–20 μ long, 8–12 μ broad at the base. Thyriothecia beginning as rounded radiate plates but early becoming elliptic, black, convex, about 250 μ wide, and when single, up to 450 μ long, often connate and longer, or Y-shaped ; basal wall subhyaline radiate, very thin and indistinct ; upper wall of subopaque radiating-longitudinal dark brown hyphae 4–5 μ thick, the cells up to 10 μ long ; margin loosely fimbriate, the fringing hyphae tortuous-radiating, mainly without hyphopodia, up to 300 μ long ; dehiscent by longitudinal fracture of the centre. Asci numerous, aparaphysate, sessile, globose to ovate, 8-spored, 50–60 × 40–50 μ. Spores conglobate, dark brown, clavate-oblong with rounded ends, smooth, 1-septate, constricted, 32–38 × 17–19 μ, the upper cell globose, the lower slightly narrower and elongate-attenuate to the rounded base. At germination the upper cell forms a single hypha on which 2 or 3 hyphopodia are formed, and from the base of which the mycelium develops, meanwhile the lower cell collapses, followed by the upper.

195. **Lembosia Lophopetali** (Rehm) Hansf., comb. n.

Syn. *Asterina Lophopetali* Rehm in Leafl. Philipp. Bot. **6**, p. 2228, 1914.

Colonies epiphyllous, black, orbicular, 0·5–1 mm. diam., scattered, thin. Mycelium of substraight to somewhat flexuous brown hyphae 4–5 μ thick, the cells mostly 25–30 μ long, branching opposite or irregular, loosely reticulate with polygonal meshes. Hyphopodia alternate or opposite, stipitate, 1-septate, straight or bent, 12–18 μ long, stalk cell cylindric, 4–8 μ long, head cell globose, ovate, cylindric or sometimes boot-shaped, usually subregular, 8–10 × 6–8 μ. Thyriothecia scattered, elliptic, straight, up to 300 × 100 μ, black convex ; basal wall hyaline, indistinct ; upper wall of opaque dark brown radiating-longitudinal hyphae 4–6 μ thick, the cells up to 10 μ long, the margin more or less fimbriate, the fringing hyphae tortuous-radiating, loose, exhyphopodiate, up to 120 μ long. Asci numerous, aparaphysate, ovate to saccate, sessile, 8-spored, 40–50 × 20–25 μ. Spores conglobate, dark brown, 1-septate, constricted, the upper cell subglobose and slightly wider than the lower which is somewhat attenuate to the rounded base, both finely verruculose ; spores 25–30 × 11–14 μ. At germination the spore forms a hyphopodium usually from the upper cell, occasionally from the lower ; the opposite cell then collapses, followed by the other as the mycelium develops from the base of the hyphopodium.

On *Lophopetalum toxicum*, Mt. Maquiling, Los Banos, Philippines, *Baker Fung. Malay. 9.* (Part of type collection.)

196. **Clypeolella Zizyphi** (Yates) Hansf., comb. n.

Syn. *Asterina Zizyphiae* Yates, in *Philipp. Journ. Sci Bot.* **13**, p. 375, 1918.

On *Zizyphus* sp., Mt. Tulaog, Tayabas, Luzon, Philippines, *Philipp. Bur. Sci. 29156* (Part of type collection) :—

Colonies amphigenous black, thin to subdense, smooth, up to 5 mm. diam., or confluent over most of the leaf. Mycelium of substraight brown hyphae 6 μ thick, the cells mostly 20–30 μ long, branching opposite or irregular, often

rectangular, at first loosely reticulate, then as the thyriothecia and conidia develop the colony becomes almost solid by repeated branching of the hyphae. Hyphopodia alternate or unilateral, sessile, continuous, hemispheric, entire 9–11 μ diam. Thyriothecia orbicular, developing below the mycelial hyphae, brown, convex, up to 170 μ diam., not fimbriate at the margin ; lower wall hyaline, indistinct ; upper wall of brown radiating hyphae 5–6 μ thick, the cells up to 8 μ long. Only immature thyriothecia are present in the specimen in Herb. Pretoria. Falcate conidia rather few, fusoid with rounded ends, dark brown, the ends cell paler, 3-septate, not constricted, the end cells much smaller than the middle cells, the apex rounded, the base subapiculate, bent, smooth, 25–30 × 10–13 μ.

This species is quite different from *Mitteriella zizyphina* Syd. which is most probably the conidial stage of a *Schiffnerula*.

PROCEEDINGS OF THE ANNIVERSARY MEETING

24 May 1948

Professor G. R. de Beer, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday 13 May 1948, having been circulated, were taken as read and confirmed.

The President welcomed the presence at the meeting of His Excellency Monsieur Erik Boheman, K.N.O., the Swedish Ambassador, and Dr. Arvid H. Uggla, Librarian of the Royal University of Uppsala.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Archibald Park Balfour, Mr. Albert Edward Blake, K.L.B., Mr. Ralph Anthony Blakelock, B.Sc., Miss Kathleen Mary Bayne, B.A, Captain Harry Walter Abbiss, M.B.E., D.C.M., M.M., Mr. Arthur Allman Bullock, B.Sc., Mr. Charles Willoughby Chew, Dr. Peter Ford, Mr. William Stuart Fraser, Rev. Arthur George Gregor, M.A., B.D., Dr. Philip Herries Gregory, Mr. Jack Raleigh Henchman Nash-Wortham, Miss Patricia Lewis, B.Sc., Mr. Henry Samuel Amos Marshall, Mr. Ernest Nelmes, Mr. David Richmond Newth, B.Sc., Dr. Rodolfo Emilio Giuseppe Pichi-Sermolli, Mr. Neville George Stephenson, M.Sc., and Dr. Henry Gerard Thornton, F.R.S.

Candidates for Fellowship were balloted for and elected :—Edward Augustine Ellis, Stanley Arthur Manning, Professor Alastair N. Worden, M.A., B.Sc., and Professor Vero C. Wynne-Edwards.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Miss E. M. Wakefield, Mr. I. H. Burkill and Mr. D. L. Burtt, as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting:—New Members of Council.—Mr. James M. Fisher, M.A., Mr. N.B. Kinnear, C.B., Prof. W. H. Pearsall, D.Sc., F.R.S., Dr. W. R. Philipson and Mr. N.Y. Sandwith, M.A.

(The retiring Councillors were Prof. T. A. Bennet-Clark, Prof. A. J. E. Cave, Dr. H. S. Holden, Mr. A. A. Pearson and Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S.)

The PRESIDENT declared the Ballot for Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting:—OFFICERS.—*President*: Professor G. R. DE BEER, F.R.S.; *Treasurer*: Colonel F. C. Stern, O.B.E., M.C.; *Botanical Secretary*: Dr. B. Barnes; *Zoological Secretary*: Dr. A. Tindell Hopwood.

In handing the Linnean Gold Medal to Dr. AGNES ARBER, F.R.S., F.L.S., the PRESIDENT spoke as follows:—

Dr. AGNES ARBER:

In awarding the Linnean Medal to Dr. Agnes Arber, the Society is honouring itself by including among the list of recipients of this Medal one whose tireless researches have adorned the subject of Botany, have advanced its frontiers, and made her the leading authority in the world on several of its aspects.

Dr. Arber's interests are wide, and I must be expected to refer to a few of them only.

First, I must mention her work on the Phyllode theory of the Monocotyledon leaf, which seeks to explain the peculiar features of the form and venation of the monocotyledonous leaf as the morphological equivalent of the petioles and phyllodes which are found in Dicotyledons. Her detailed investigations showed that the leaf anatomy strongly supported this theory, provided an explanation of the existence of a single cotyledon in the embryo, and served to extend greatly the comparative basis of such studies.

Dr. Arber's interest in the Monocotyledons led her naturally to a long series of studies on the Grasses, which resulted in the publication of her book on the Gramineae. This was followed by a comprehensive work on the Monocotyledons dealing with the general background of the whole group.

In the course of these investigations, Dr. Arber acquired a very large amount of information about water plants, which she brought together in her book on Water Plants. This summarizes the special types of investigation in which she has been engaged, and is a mine of information relating to the biology of water plants.

Dr. Arber's work has consistently been marked not only by an intimate personal knowledge of the subjects with which she has dealt, but also by its wide cultural background based on a very extensive knowledge of the history of botany. This is shown in her delightful book on Herbals, and in her fascinating study of Goethe and his doctrine of the metamorphosis of plants.

We are looking forward with great interest to Dr. Arber's forthcoming work on the general principles of Morphology.

Not the least attractive and valuable feature of Dr. Arber's numerous works are the beautiful illustrations from her own hand which accompany them.

We are proud that Dr. Arber, a Fellow of our Society, should be the first Lady Botanist to be elected into the Fellowship of the Royal Society, and as a token of our esteem for her services to Science I have great pleasure in handing to her the Linnean Medal.

In reply, Dr. Arber expressed her profound appreciation of the honour that had been conferred upon her.

The PRESIDENT then spoke as follows on the recipients of the Trail Award and Medal, Dr. CYRIL DEAN DARLINGTON, F.R.S. and Dr. HONOR BRIDGET FELL, F.L.S., and made the presentations:—

Dr. Cyril Dean Darlington :

By bringing together critical judgment, sound philosophical imagination, and a formidable mass of new observations, it has been given to Dr. Darlington to make permanent contributions to the very foundations of knowledge in the fields of nuclear cytology, genetics, and evolution, in animals and plants.

Dr. Darlington unravelled the bewilderingly complex relations between the phenomena of mitosis and meiosis which lie at the basis of the division of every cell and the formation of every gamete. He provided an objective explanation of the behaviour of chromosomes and of the mechanism of crossing-over, which supply the physical basis for the modern theory of genetics. He has shown that the series of events in meiosis involving the pairing, torsion, reproduction, crossing-over, co-orientation and segregation of the chromosomes can be placed in a causal sequence. He has investigated the relations between genes and the nucleic acids, and thrown so much light on these fundamental aspects of what used to be called the properties of protoplasm that it is particularly appropriate that he should be the recipient of the Trail Award.

Dr, Honor Bridget Fell :

Complete mastery of the very difficult and complicated technique of tissue-culture, a deep and critical knowledge of the problems involved, together with a rare insight into the bearing of her results on general principles of development, have enabled Dr. Fell to make lasting contributions to knowledge in the fields of embryology, histology, and morphogenesis.

Dr. Fell has supplied the most critical and objective description of the processes of ossification in cartilage yet available. Her cultures of rudiments of various embryonic structures have yielded information of great interest and importance concerning the powers of differentiation of tissues. By adapting her technique to the experimental investigation of the developmental powers of tissues from genetically abnormal material, she has been able to throw light on some of the problems attending the way in which genes exert their effect on the tissues. These also are aspects of the fundamental properties of living matter for which reason the Linnean Society is proud to include the name of Dr. Honor Fell among those of recipients of the Trail Award.

LIBRARIAN AND ASSISTANT SECRETARY'S REPORT

List of the Society.—Since the last Anniversary Meeting the Society has lost 25 members. The detailed statement is as follows :—

12 *Fellows by Death.*—The Lady Isabel M. P. Browne, George Matthai, Emily Mary Berridge, Sir Albert Howard, Kt., C.I.E., Francis E. Lloyd, Ben Wells, Herbert W. Pugsley, Charles C. Hurst, Bernard S. Dyer, Edith I. Grindley, Frederick Orpen Bower, J. L. Chaworth-Musters.

2 *Foreign Members by Death.*—Edouard Chatton, P. A. C. Dangeard.

1 *Fellow by Withdrawal.*—Herbert Ashby.

6 *Fellows by Removal from the List.*—P. J. Gregory, H. C. Javaraya, Rajkumar Sen, K. V. Srinath, Mohammad Sharif.

During the Session 89 Fellows have been elected ; 67 have qualified. 2 Foreign Members have been elected. The present number on the list of qualified Fellows is 716.

Library.—Between the 1 May 1947 and the 30 April 1948, 20 books have been presented ; 25 books and 133 parts of periodical publications and 92 reprints have been purchased. During the same period the number of volumes bound was 188.

The number of volumes borrowed by Fellows and Associates was 1178, and by the National Central Library 232. 679 signatures were recorded in the Library Visitors' Book.

A beginning has been made with the classification of works in the Library by the use of the Bliss Classification.

Linnaean and Smithian Collections.—Since the return of the Linnaean Collections from safe storage they have been consulted in an increasingly frequent number of times; the greatest number of consultations being those relating to the Herbarium.

Some progress has been made with the compilation of a Catalogue of the Smithian Herbarium. It is hoped to complete and publish this during the coming twelve months.

THE PRESIDENT'S REVIEW

We are honoured today by the presence of His Excellency the Swedish Ambassador, Monsieur Erik Boheman, and Dr. Arvid H. Uggla, Librarian of the University of Uppsala, who has come to spend some months with us working on the Linnaean Manuscripts. In welcoming them I should like them to feel assured that they and their countrymen will never be strangers in our midst.

In passing in review the salient events of this, the 160th Session of the Society, I should like to begin by referring to two of the many benefactions which the Society has received. In particular I desire to place on record the gratitude of the Society for the generous gift of £2500 from the Pilgrim Trust, to serve as a nucleus for the sum of £10,000 which we hope to raise for the restoration of the Library. And the Library itself has been enriched by the gift of a manuscript Notebook of Thomas Lawson, presented to the Society by Mr. Reginald Hine, F.S.A.

Referring now to the meetings of the Society, we have had the good fortune to enjoy two Discussion Meetings of especial interest; one on Systematics held in conjunction with the Association for the Study of Systematics, and the other on the Homing and Migration of Birds. So successful were these meetings in stimulating interest and attracting a distinguished audience of guests, that plans have been made for the holding during next Session of half-a-dozen such meetings on various subjects.

I wish also to refer with great pride to the Hooker Lecture which was delivered on 29 April by Professor D. M. S. Watson, F.R.S. I have a particular reason to be especially grateful to Professor Watson, for after a discourse of so authoritative and fundamental a nature by such a master, I have considered that I was doubly justified in availing myself of the dispensation whereby Presidents are not called upon to deliver more than one Presidential Address.

I have also to report that during the Session the Society, again in conjunction with the Association for the Study of Systematics, tried the experiment of organizing a set of Lectures on the Principles of Taxonomy. Twelve such lectures were delivered by the most distinguished authorities in various fields of Taxonomy to audiences of students of the University of London. I have been pleased to learn that these lectures were greatly appreciated, and it is hoped that a similar course may be held during the next Session.

In pursuance of its vigilant watch over the preservation of nature reserves, the Council of the Society appointed Captain Cyril Diver, C.B.E., and Mr. A. H. G. Alston as its representatives to attend the Public Local Enquiry at Wareham on 16 March 1948 in connexion with the Lulworth and East Holm Services Training Area, and we very much hope that when the findings of that Enquiry are known, they will be found to have benefited by the advice of the representatives of this Society.

The number of new Fellows elected during this Session, 89, is a gratifying confirmation of the vigour of the Society and all that it stands for. But I am not content to let the matter rest at that, and I wish again to appeal to all Fellows to consider carefully whether in the circle of their friends and acquaintances there may not be some suitable persons for candidature of the Fellowship of the Society. We are passing through a difficult period, particularly in regard to the maintenance of the service of publications by the Society. As matters stand today, the Treasurer and the President have to go, hat in hand, and beg for money from the Parliamentary Grant in aid of Scientific Publications, and I am glad to say that we have not been wholly unsuccessful. But I consider that a Society such as this, with all that it stands for, should be shielded from financial dependance on other sources. Our Fellowship stands today at 750. I shall not be satisfied so long as it remains under 1000. It is up to every three Fellows during the coming session to find one suitable candidate between them, for I want 250 more.

I wish to express my gratitude for the loyal help and support which I have enjoyed during the Session from the Vice-Presidents, the Officers, and the Staff of the Society, and this leads me to the only topic on which I have to speak with regret, which is the resignation of Dr. Malcolm Smith from the Office of Zoological Secretary. For nine years he has served the Society with unstinted devotion and success, and the difficulties of his years of office were doubly increased by the war and what has followed it. I am sure that you would like me to wish Dr. Malcolm Smith every happiness in his retirement and to express the hope that we shall continue to see him at our meetings.

The President read a telegram just received from the President of the Swedish Linnean Society (Svenska Linné-sällskapet), announcing that that Society had elected Mr. SPENCER SAVAGE, F.L.S., an Honorary Member.

The Financial Report was given by the Treasurer as follows, and the Accounts of the Society, duly audited, for the year 1947–48 were laid before the meeting.

TREASURER'S REPORT.

Printed copies of the Treasurer's Accounts for the Financial year which ended on 30 April 1948 are before the Meeting. A Statement has been prepared by the Auditors who certify as to detail; the Audit Committee has inspected the books, verified the investments and passed the accounts; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items :—

The main increase is in the sales of publications, which has gone up from £134 to £693 which is no doubt due to Scientific Societies and others making up their back copies which they had not bought during the War. £750 was received as a grant-in-aid of publications from the Royal Society as against £800 received in the previous year. The actual increase of income on the year was £592—largely composed of the increase of sales of publications.

On the payment side of the accounts there have been several small increases amounting in all to an increase of expenditure of £138. The Council have decided to place £900 to a Reserve for Publications which I will explain. This leaves a balance of £581 to be carried forward to 1948–49.

Last year the Society had a reserve of £1700 for publications in hand but not yet printed. Of this sum £596 has been expended, leaving £1103 in reserve. I estimate that the Society's publications, including the late Mr. Pugsley's Monograph on British *Hieracia* and the Calendar of the Manuscripts of John Ellis (*c.* 1705–76) will cost £2440—it may be more if the cost of printing further increases. To meet this cost there is £1100 reserve of 1947–48 and £450 to come from the General Fund, leaving £900 to find for which a reserve has been

found from the balance of the General Fund this year. The balance of the Publications Reserve Fund standing at £2003 is shown in the balances of the Special Accounts.

On the next page, among the Special Accounts, on the right-hand side is recorded the balance of the Reserve Account of £1286. This sum is being expended on the redecoration of the hall and stairs, electrical and sundry repairs, already completed, and on the larger item, the renewal of the Central Heating System. This work on the Central Heating will start at once and it is hoped that it will be ready by next winter. Our present heating system was put in many years ago—in 1873.

Another item is recorded for the first time in the accounts, the Library Restoration Fund. The Council found that, owing to the War and the deterioration due to war conditions, there was a great deal of leeway to make up in the Library to bring it up to date. The Library, with its 70,000 volumes and all the wonderful original books and Manuscripts of Linnaeus, is one of the great biological libraries in the world. The Council found that if everything was done that was necessary in the Library the cost of routine binding, including arrears of war-time issues of periodicals and works (£1000), rebinding, rebacking and repairs of existing books (£3000), purchase of war-time issues of foreign periodicals and works (£1500), new shelving and structural alterations to accommodate the shelving and cost of labour to remove books to new shelving, new boxes for pamphlets and separate copies (£1250), and new floor-covering and decorations and furniture renovation, etc., a sum of £10,000 would be required. The Council decided, therefore, to open a new Fund. The Pilgrim Trust was approached, and after carefully enquiring into the position of our Library and its value to biologists, has opened the Fund with a very fine donation of £2500, for which I am sure all Fellows will be grateful. Already £630 has been expended on Library shelving, glazing of book-cases and structional alterations to make room for the new shelving on the upper floors, and I should like to ask all friends of the Linnean Library to help this fund in any way they can, by donations or legacies, in order that this historic library can be maintained and conserved.

Finally, on the last page of the accounts will be found the list of Investments. The only important changes are in the English Railway Stocks which have been converted by the Government into British Transport Stock. The Society has only lost about £10 per annum on Income and has gained about £58 on the nominal value of the Stocks. The market value of the gilt-edge stocks has fallen since last year, but this is only of academic interest as the income remains the same.

I should like to thank Mr. O'Grady, our Clerk, for the excellent manner in which the accounts have been kept. Mr. O'Grady carries out the detailed work in keeping the accounts, and I am grateful to him for the conscientious way in which this work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

Special Accounts
(Trust and Reserve Funds)

Receipts	£	s.	d.	£	s.	d.
To Balance at 1 May 1947 :—						
Westwood Fund	82	1	1			
Trail Award Fund	43	9	2			
Crisp Award Fund	73	0	2			
Hooker Lecture Fund	118	0	2			
Goodenough Fund	3	2	8			
Minchin Fellowship Fund	6	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve Fund	1387	7	8			
Reserve for Publications Fund	1700	0	0			
				3832	14	11
,, Transfer from General Account :—						
Reserve for Publications Fund		....		900	0	0
,, Interest on Investments (including Income Tax recovered) :—						
Westwood Fund	10	17	5			
Trail Award Fund	3	10	0			
Crisp Award Fund	10	5	0			
Hooker Lecture Fund	21	18	0			
Goodenough Fund	8	12	8			
Minchin Fellowship Fund	3	0	0			
Staff Pension Fund	9	10	8			
				67	13	9
,, Grant from Royal Society (expenses of Dr. Uggla's Visit)		....		200	0	0
				£5000	8	8

Payments	£	s.	d.	£	s.	d.
By Hooker Fund :—Lecturer				26	5	0
,, Reserve for Publications Fund :—						
Transfer to General Account		....		596	10	0
,, Reserve Fund :—						
Chairs and re-upholstering		....		100	15	0
,, Staff Pension Fund :—						
Purchase of £7 15s. 0d. 3 per cent. Savings Bonds 1955/65		....		7	17	2
,, Balance at 30 April 1948 :—						
Westwood Fund	92	18	6			
Trail Award Fund	46	19	2			
Crisp Award Fund	83	5	2			
Hooker Lecture Fund	113	13	2			
Goodenough Fund	11	15	4			
Minchin Fellowship Fund	9	10	5			
Carnegie Corporation Grant	419	3	7			
*Reserve Fund	1286	12	8			
†Reserve for Publications Fund	2003	10	0			
Royal Society Grant	200	0	0			
				‡4267	8	0
Staff Pension Fund, at Bank of England for investment		....		1	13	6
				£5000	8	8

* Estimated cost of repairs (1946), renewal of central heating installation (1948), and sundry repairs and decorations completed or in hand (£1129).

† Amount set aside to meet cost of Publications in hand.

‡ Including £4002 15s. 0d. in Post Office Savings Bank.

Treasurer's Accounts for the

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

General

Receipts	£	s.	d.	£	s.	d.
To Balance at 1 May 1947 :—						
Current Account at Bank	81	1	5			
Deposit Account Post Office Savings Bank	541	18	7			
Cash in hand	12	0	3			
				635	0	3
,, Admission Fees				120	0	0
,, Arrears of Annual Contributions	70	0	0			
,, Annual Contributions for year	2201	18	0			
Do. in advance	69	10	0			
				2341	8	0
,, Do. of Associates				18	1	0
,, Composition Fees				182	0	0
,, Interest on Investments (including Income Tax recovered)				325	2	11
Do. Post Office Savings Bank Account				117	4	5
,, Premium on Stock converted				10	0	0
,, Sales of Publications :—						
Transactions	166	1	1			
Journals	318	12	4			
Proceedings &c.	208	17	10			
				693	11	3
,, Grant in aid of Publications				750	0	0
,, Miscellaneous Receipts				59	14	4
,, Transfer from Reserve for Publications Fund				596	10	0
				£5848	12	2

Library

	£	s.	d.
To Balance 1 May 1947	169	6	1
,, Interest on Investments (including Income Tax recovered)	47	6	11
,, Donation	10	10	0
,, Transfer from General Account	300	0	0
	£527	3	0

Library

	£	s.	d.
To Grant, The Pilgrim Trust	2500	0	0
,, Anonymous Donors :—			
Transfer from Library Account (1946–47)	100	0	0
Received during year	15	0	0
	£2615	0	0

Fellows' Postal

	£	s.	d.
To Balance at 1 May 1947	50	6	5

YEAR ENDED 30 APRIL 1948

Meeting, 24 May 1948)

from 1 *May* 1947 *to* 30 *April* 1948.

Account

PAYMENTS	£	s.	d.	£	s.	d
By Coal, Electric Current, and Gas				163	10	6
,, Repairs: Sundry				50	15	6
,, Taxes and Insurance				70	7	7
,, Miscellaneous Printing and Stationery				251	2	5
,, Petty Expenses and Postages				281	17	11
,, Publications :—						
Printing	1105	10	5			
Illustrations	143	10	9			
Distribution	97	8	10			
				1346	10	0
,, Transfer to Reserve for Publications Fund				900	0	0
,, Salaries, Wages, etc.				1466	16	8
,, 'Zoological Record' (Vol. 83) Donation				15	0	0
,, The Biological Council—Donation				5	5	0
,, Staff Annuities (Annual Premiums)				100	0	0
,, Purchase of £274 5*s.* 5*d.* 3 per cent. Treasury Stock (Compounders' Fees)				274	0	0
,, Illuminated Vellum (Hon. Member)				15	0	0
,, Linnean Medal (1947)				26	15	3
,, Transfer to Library Account				300	0	0
,, Balance at 30 April 1948 :—						
Current Account at Bank	117	18	3			
Deposit Account Post Office Savings Bank	456	8	0			
Cash in hand	7	5	1			
				*581	11	4
				£5848	12	2

* Including £8 Composition Fees awaiting investment.

Account

	£	s.	d.	£	s.	d
By Transfer to Library Restoration Fund (Donation 1946/47)				100	0	0
,, Periodicals				177	6	1
,, Binding				93	3	6
,, Books				30	2	8
,, Balance at 30 April 1948. Current Account	26	10	9			
,, Deposit Account Post Office Savings Bank	100	0	0			
				126	10	9
				£527	3	0

Restoration Fund.

	£	s.	d.
By Balance on Deposit 30th April 1948	*2615	0	0
	£2615	0	0

* Expenses incurred but not yet paid, Library steel shelving, alterations and renovations, £630 3*s.* 7*d.*

Account

	£	s.	d.
By Balance at 30 April 1948	50	6	5

Investments on 30 April 1948

General Account

£	s.	d.			*Market Value 30 April 1948.* £	s.	d.
1000	0	0	3½ per cent. London County Consolidated Stock 1958–68	@105	1050	0	0
1548	8	9	British Transport 3 per cent. Guaranteed Stock 1978–88	@ 96	1486	10	0
338	6	8	3½ per cent, War Stock	@102	345	2	0
1000	0	0	2½ per cent. Defence Bonds	@100	1000	0	0
2199	18	6	4 per cent. Australian Stock 1961–64	@110½	2430	18	4
200	0	0	3 per cent. War Stock 1955–59	@104	208	0	0
1139	13	0	3 per cent. Savings Bonds 1955–65	@102	1162	8	10
2310	16	10	2½ per cent. Consolidated Stock	@ 76½	1767	15	10
176	19	3	3 per cent. Savings Bonds 1960–70	@100½	177	16	11
274	5	5	3 per cent. Treasury Stock	@ 93½	256	8	10
					£9885	0	9

Library Account

£	s.	d.			£	s.	d.
471	18	9	British Transport 3 per cent. Guaranteed Stock 1978/88 (Bentham Bequest)	@ 96	453	1	2
103	12	5	Surrey County 3 per cent. Stock 1961–66 (Wakehurst Bequest)	@101	104	13	2
191	12	7	4 per cent. Australian Stock 1961–64 (Walker & Morey Bequests)	@110½	211	15	0
107	2	1	2½ per cent. Consolidated Stock (Stebbing Bequest)	@ 76½	81	18	8
530	0	0	3 per cent. Savings Bonds 1960–70 (Tagart Bequest)	@100½	532	13	0
					£1384	1	0

Special Accounts

£	s.	d.			£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent. "B" Stock (Westwood Bequest)	@ 93	215	19	10
	667	14	2	Ditto ditto (Hooker Lecture Fund)	@ 93	620	19	5
	163	11	5	Ditto ditto (Goodenough Fund)	@ 93	152	2	5
	100	0	0	New South Wales 3½ per cent. Stock 1930–50 (Trail Award Fund)	@103	103	0	0
	409	11	1	2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 76½	313	6	2
£380 10 6	156	7	2	,, ,, ,, (Westwood Fund)	@ 76½	119	12	3
	74	14	6	,, ,, ,, (Hooker Lecture Fund)	@ 76½	57	3	3
	149	8	10	,, ,, ,, (Goodenough Fund)	@ 76½	114	6	5
	268	0	2	3 per cent. Savings Bonds 1955–65 (Staff Pension Fund)	@102	273	7	4
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@100½	100	10	0
						£2070	7	1

F. C. STERN, *Treasurer.*

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1948 and found them correct. We have verified the Investments and Bank Balances.

Dated this 19th May 1948.

W. B. KEEN & Co., *Chartered Accountants,*
Finsbury Circus House,
Blomfield Street, London, E.C.2.

G. R. DE BEER,
B. BARNES,
I. H. BURKILL,
A. TINDELL HOPWOOD,
H. W. PARKER,
ELSIE M. WAKEFIELD,
} *Audit Committee.*

On a motion by Dr. J. RAMSBOTTOM, O.B.E., seconded by Dr. H. A. BAYLIS, the Report and Statement of Accounts were adopted.

Two films, entitled 'The South African Clawed Toad (*Xenopus laevis*)', and 'Notes on the life-histories of Boas and Pythons'; with commentaries by Dr. EDWARD HINDLE, F.R.S., were then shown. The President expressed the thanks of the meeting to Dr. Hindle.

The PRESIDENT then declared the Session of 1947–48 ended.

NON-SEXUAL REPRODUCTION IN SPONGES, WITH SPECIAL REFERENCE TO A COLLECTION OF YOUNG GEODIA

By MAURICE BURTON, D.Sc.,
Department of Zoology, British Museum (Natural History).

(Plates **1–3** and 7 text-figures.)

[Read 16 October 1947.]

While searching the collections of *Geodia* in the British Museum for evidence which might throw light on the reproductive process in this genus, my attention was drawn to two jars containing a number of small specimens which seemed worthy of careful study. Clearly they were immature, and a brief examination was sufficient to suggest that their form and appearance was a little unusual. As the examination proceeded it seemed more and more probable the 100 or so small individuals in these jars indicated the possibility of a novel method of vegetative reproduction. The observations which followed, and the conclusions drawn from them, are set forth below, but before dealing with these it may be advisable to summarize our present knowledge of non-sexual reproduction in sponges.

The literature devoted to development in sponges is fairly extensive, and in addition there is a number of scattered references to the finding of embryos, larvae, buds and the like. A survey of these gives the impression that although sexual reproduction has been described beyond doubt, the great majority of cases of supposed sexual development lack confirmation of the vital phases, namely the production of spermatozoa and the actual fertilization. On the other hand, the suggestion, notably by Wilson (1894), that gemmules differing in no recognizable feature from sexually-formed embryos may occur, serves to leave in doubt how many truly authentic instances of the sexual method have been recorded. Added to this is the fact that asexual or vegetative processes are known commonly to occur in a number of species. In other words, one gets the impression that non-sexual reproduction (*i.e.* asexual or vegetative) preponderates. In describing an alleged new method of non-sexual reproduction in *Geodia barretti*, therefore, it may be profitable to review the present state of our knowledge of reproduction in the phylum as a whole.

Undoubted ova, together with the early stages of segmentation, have been recorded by several authors, notably by Schulze (1875, 1879, 1880), but apart from this, records of ova are mainly to be found in occasional references in the text of systematic papers. Spermatozoa, likewise have been recorded by

Schulze (1877, 1878) ; Sollas (1888, pl. xli, figs. 13–19), and later, in a more convincing manner by Gatenby (1920) which is subsequently confirmed, in part at least, by Duboscq and Tuzet (1937).

Sexual dimorphism appears to be non-existent and the only attempt to analyse the ratio of the sexes was made by Gatenby (1920, p. 285) who comments : ' In only one case out of twenty-five . . . was the sponge a positive hermaphrodite, and in all the other examples . . . only oogenesis stages were discovered '. This seems a sufficient reason for the paucity of reliable records of spermatozoa and spermatogenesis.

Against this relatively scanty information of the occurrence of spermatozoa, ova, and cleavage stages must be set the work of Wilson (1894) on the asexual origin of ciliated larvae, and the quite extensive records of budding, gemmule-formation and related processes. In addition, there are those instances in which the reproductive process in whole families is known to us only from occasional records of buds, as in the families Stellettidae, Geodiidae, Clavulidae and others ; or examples like the Tethyadae, where numerous cases of buds can be seen but only two or three records of ova exist. Finally, apart from records of buds and Ijima's (1904) account of the development of larvae from groups of ' archaeocytes ', reproduction in the Hexactinellida would be unknown to us, but for Okada's (1928) description of the development of larvae from ova in *Farrea sollasii*.

Our knowledge of the reproductive processes in sponges may therefore be summarized : there is relatively little reliable information of the occurrence of ova and true segmentation stages, and an abundance of scattered information suggesting that non-sexual reproduction predominates, particularly in species inhabiting the deeper waters (say, below 20–30 fathoms). On the other hand, it is possible that the sexual process is more widespread than appears to be the case, and that more work of the quality of that of Dendy, Gatenby, Okada, Duboscq and Tuzet will ultimately prove this to be so.

Summary of the various Non-sexual Processes.

The non-sexual reproductive processes may be listed as :—

(1) The production of asexual ciliated larvae which, in their later stages, differ in no observable particular from sexually-produced larvae ;
(2) The formation of buds ;
(3) The formation of resistant, non-ciliated gemmules ;
(4) Fragmentation.

(1) *The production of asexual ciliated larvae.*—Wilson published his first observations on this in 1891 but gave a more comprehensive account in 1894. Briefly the process consists in the appearance within the internal tissues of amoebocytes, filled with a granular yolk, which collect together in groups and, later, by cell-division, produce the normal spherical embryo. This embryo then proceeds in a manner normal for the sexually-produced larva until the free-living state and ultimate metamorphosis are reached. Wilson's work was criticized by Mass (1896) and Minchin (1897), but was upheld by Ijima (1901), the contending arguments being reviewed by Wilson in 1902. It is of interest to note that, in both sexually- and asexually-produced larvae, the process does not necessarily take place simultaneously throughout the body nor in consistently localised areas, but groups of embryos may appear at any point. Associated with the formation of the asexual embryos is a degeneration of the surrounding tissues and, especially, of the flagellated chamber. In view of the observations by Dendy (1915), Gatenby (1920) and Duboscq and Tuzet (1937) that the ovum is derived from a collared-cell, it would appear that the breakdown of flagellated chambers

has more than a mechanical significance, and that this degeneration offers direct support to Wilson's interpretation. Moreover, a number of embryos observed by me in the course of my systematic work showed no sign of the regular cleavage such as is figured by Schulze (1877) and Burton (1932), for example. It is possible, therefore, that the formation of asexual ciliated larvae is a fairly general process, although more work is obviously needed on this important aspect of development.

(2) *The formation of buds.*—The outstanding example of this process is found in *Tethya*. Eichenauer (1915) has shown that in *T. aurantium* (Pallas) amoebocytes, charged with granular material, migrate along the radial bundles and assemble in outgrowths of the cortex to produce buds, which later become detached and float away. A similar process has been described by Arnesen (1917) for *Polymastia mammillaris* (Müller).

As an indication of the quantitative relationship between sexual and asexual reproduction in these, and other species, it may be noted that in my examination of several hundreds of samples of *Tethya*, something like fifty per cent. of the specimens bore buds or showed signs of recent budding. Moreover, it appears probable that budding may take place throughout the year. The sexual process, on the other hand, is represented by five records only of ova (one in Sollas 1888, pl. xliv, figs. 5–6 ; four in Burton 1925, p. 25). In *Polymastia mammillaris*, on the other hand, budding is not common and records are comparatively rare. According to Arnesen (*l.c.*) it is confined to July, August, and September, the normal breeding months for sponges in the northern hemisphere. Another contrast may be made between *Polymastia* and *Tethya*, for in the latter, in addition to the five records of ova, embryos have been recorded (Burton 1925) in a species which does not appear to reproduce by budding, namely *Tethya magna*. From the available evidence it might be doubted whether *Polymastia* would produce sexually-formed embryos simultaneously with asexual buds, and the records show that the eggs are produced in August, September and October, so that sexual and non-sexual seasons may overlap for a given population, though probably not for any given individual.

The formation of buds has been noted in other species, as for example, in a few species of *Leucosolenia* and in the Hexactinellida (*cf.* Schulze 1887, pl. liv, fig. 1), but it is not known what histological changes occur in these cases. In addition there are species in which bud-formation is accompanied by fragmentation, but so little is known of the process that more cannot be said here.

(3) *The formation of resistant, non-ciliated gemmules.*—The outstanding example of the formation of resistant, non-ciliated gemmules is found in freshwater sponges, in which all species reproduce predominantly by this method, although sexual reproduction has also been recorded. There seems to be little doubt that some marine species also produce resistant gemmules. *Suberites domuncula*, for example, produces a layer of gemmules, each surrounded by a coat of spongin. These, presumably, form new individuals on the death of the adult. The stages leading to their formation, and their development subsequent to the death of the parent have, however, never been studied.

Similar basal layers of resistant gemmules have been described for *Suberites carnosa*, and it may be that this form of reproduction is more common than the records indicate. The fact that the gemmules are laid down in contact with the substratum means that specimens, and especially those brought up in the dredge, are liable to have been brought away without the basal tissues so that in many cases the gemmules are left behind. Where the sponge grows on a substratum which is itself removable, as in *Suberites domuncula*, there is a greater chance of a basal layer of gemmules being seen. An illustration is

furnished by a specimen of *Haliclona* from the Arctic (Plate **3**, figs. 1 and 2) growing on *Zostera*. This is the only known example of gemmules in the Haploscleridae, to which *Haliclona* belongs, and this specimen is almost the only one to be collected with its substratum.

(4) *Fragmentation*.—Vegetative reproduction by fragmentation has been used in the experimental culture of commercial sponges, and in certain laboratory experiments on non-commercial species, but there are no records of this process occuring naturally. A supposed process of vegetative reproduction in *Grantia compressa* has, however, been observed by me and it is hoped that more extensive notes will be published at a later date. This takes the form of a natural hypertrophy at certain points on the body which is followed by fission.

There is, however, a second form of fission to which attention might be directed. So far little is known of this, but the following illustration indicates the form it may take. Some years ago, the sandy shore at Littlehampton, Sussex, was littered during October with thousands of rounded masses of *Halichondria*. None of these showed any sign of having been attached and eventually they were washed away from the beach. There can be little doubt that they had been washed in from the deeper offshore waters by the storms which had just ended. Such is the observation, and it is not possible to do more than guess at an explanation : that they were fragments of *H. bowerbanki* broken off by wave-action, that the injured surface had been regenerated and that, possibly, some of them would in time become attached and grow into mature sponges (see Plate **3**, figs. 1 and 2).

How far such an accidental breaking-up may contribute to the reproductive total of a species it is impossible to say. At least this may be added, that I have during 1947 paid particular attention to this point in field-observations, and have found *Adocia cinera* and *Hymaniacidon perlevis* being broken up by wave-action.

Résumé.—These notes can do little more than indicate the existence of three main methods of non-sexual reproduction, and suggest that there may be a fourth. There is sufficient evidence in them, however, to suggest that non-sexual reproduction may play a larger part in the phylum Porifera than has hitherto been suggested.

A Suggested Origin of the Young *Geodia*.

Although, as has been pointed out, there are numerous references to the adult sponges as a whole, it is noteworthy that there has been no mention of either larvae or buds from the several hundreds of specimens of Geodiidae recorded, except for two accounts of the formation of buds in *Geodia eoaster* by Topsent (1892, pl. v, fig. 9 ; 1904, pl. iv, fig. 7). This makes it more interesting, therefore, to report upon a hundred or so specimens, of 1 to 2 mm. diameter, from an unspecified point in the Arctic, presumably picked out of the mud and to speculate upon their origin and formation. On the one hand, we have the familiar adult *Geodia* ; on the other, we have these very young specimens, with no direct data to help in reconstructing the link between the two. There are, however, some striking features of both adults and young which enable us to postulate a theory on asexual reproduction in this genus.

In the first place, it is necessary to show why the young specimens should not be immediately accepted as normal post-larvae, developed from the usual sexually-formed larvae. Perhaps the strongest argument here rests in the large number found. Young individuals have been obtained before but it is unprecedented for so large a number to be taken in a single catch, the reason being presumably that free-swimming larvae tend to be dispersed and the resulting post-larvae scattered. Then, their irregular shape contrasts sharply with the

perfectly globular form of the few post-larval *Geodia* (of 2 to 3 mm. diameter) hitherto found. In a nearly allied family, the Tetillidae, in which the sexual development is better known, the post-larvae are again very regular in shape. The final and perhaps strongest argument is the presence of large spicules, either singly or in fair numbers, passing through the bodies of the young sponges and protruding, often in many directions at once, well beyond the surface. This last condition could only be attained in post-larvae derived from free-swimming larvae if it could be imagined that such larvae had settled on discarded adult spicules lying on the sea-bottom. This would demand, however, a behaviour without known parallel, and, in addition, a greater concentration of such spicules on the sea-floor than we have reason to believe from the evidence of soundings.

If the young sponges under examination do not result from sexually-formed, free-swimming larvae, it can only be assumed that their origin is from buds formed on the surface, as in the nearly related *Tethya* and *Polymastia*, or from some process hitherto unknown. Arguments against their being surface buds are seen in the complete absence of traces of such budding in all but one specimen of *Geodia*, whereas in *Tethya* either the buds or their stalks are seen in 70 to 80 per cent. of specimens so far recorded, and in *Polymastia*, in which equally with *Geodia* so very little is known of the reproductive processes, at least a few buds have been found attached to some adults. Finally, it is difficult to believe that bud formation, as a normal and frequent procedure, is mechanically possible in view of the presence in *Geodia* of the thick cortical layer of closely-packed siliceous spicules. There is normally an absence of projecting megascleres such as make the migration of amoebocytes well beyond the surface possible, as in *Tethya* and *Polymastia*. In my opinion, the presence of the cortical barrier of sterrasters has contributed to the evolution in *Geodia* of vegetative reproduction not previously suspected. Such a process may conceivably operate in species belonging to other genera, but could quite well have developed to meet the special circumstances created by the presence of the dense cortex.

Before elaborating this line of argument it is necessary to recall Sollas's view that sponges periodically extrude their spicules. Until a few years ago, this view depended entirely upon slender circumstantial evidence. Then (1931) I drew attention to some specimens of *Cinachyra barbata* and *Polymastia invaginata* which were shaggy with projecting megascleres while the others had a smooth non-hirsute surface, as though they had moulted. At the same time I quoted the observations made by Mr. Rayner on board the R.R.S. ' Discovery.' Recently, I have discussed this matter again with Mr. Rayner who amplified his previous remarks. Although the notes he made at the time are not available at this moment, his account, given from memory, is that he took a large sponge, of unknown identity, with the surface covered with long, projecting megascleres. He rubbed the spicules off so that the surface was almost smooth, and in a short while the projecting megascleres had been renewed. Three pieces of wire were driven through the body of the sponge at different angles so that no matter in what position it rested, it was supported from contact with the surface of the vessel in which it was contained. To quote from Mr. Rayner's conversation : ' The renewal of the projecting spicules was very rapid. Speaking from memory they were extruded in something of the order of two inches in about half-an-hour'.

Since last writing on this subject, I have carried out an experiment with a *Haliclona* sp. found growing in the filter-beds of the Aquarium of the Zoological Society of London. A large glass dish was taken, thoroughly cleaned, and filled with filtered sea water. Into this a specimen of the *Haliclona* was placed as gently as possible and the whole left undisturbed for two weeks. At the end, the sponge was replaced in the filter-bed and continued to live for several months,

which gave clear proof that the results obtained were not due to a moribund condition. The water was poured off and the bottom of the dish examined with a low power binocular microscope. It was coated with a close-meshed irregular network composed of spicules proper to the *Haliclona*, the fibres of this network being kept together by a more or less continuous tissue of cells. The only possible explanation can be that in two weeks the *Haliclona* had extruded spicules of something like twice the quantity normally comprising its skeleton, according to my rough estimate at the time. Moreover, living cells had also escaped, apparently, at the same time as the spicules, and had combined to arrange the spicules in fibres and in a reticulation comparable with that normally found in the body, except that the meshes were larger and more irregular, and the fibres thicker than usual. In addition the cells had remained to bind the spicules together. Doubtless the moulting of the spicules is accomplished by amoebocytes acting as transporters, which are themselves carried out of the body. Unfortunately, it was not possible to continue the experiment to see whether the extruded amoebocytes would form regenerative cell masses, but this is what could be expected by analogy with the behaviour of the amoebocytes which form the surface buds in *Tethya*.

To return to the young specimens of *Geodia*, it is possible that as the megascleres of the adult are being extruded, amoebocytes are also carried away and in the comparatively still waters of the deep seas, the normal habitat for species of this genus, the opportunity would occur for the regenerative cell masses to be formed around one or a few of the parental spicules leading to the formation of young sponges.

Several specimens of (preserved) *Geodia* with hirsute patches on the surface have been examined in the hope of identifying amoebocytes on the free surfaces of the extruded spicules, but nothing was seen that could be positively identified as such, largely because of the presence of an appreciable quantity of fine débris.

The experiment carried out on *Haliclona* should be repeated on other species under laboratory conditions to see whether young sponges would arise from the extruded amoebocytes. If successful, such experiments would provide valuable collateral evidence for the view suggested here of the origin of the young Arctic *Geodia*.

Description of the Structure of young *Geodia* and a Comparison with the known Structure and Formation of Regenerative Cell Masses.

The 100 specimens of *Geodia barretti* (pl. i) were all taken in a single haul at an unspecified point in the Arctic, and from an unknown depth. They are all pale yellow and are roughly of three shapes : (*a*) spherical or nearly so, (*b*) navicular, or (*c*) irregular, consisting of rounded and navicular lobes. The spherical or subspherical specimens range from 1·5 mm. to 6 mm. in their longest diameter, the navicular from 3 to 8 mm. long. The irregular or compound specimens are larger, and the biggest of them is 6 by 10 mm.

All the specimens have in common certain features which are not readily seen in the photographs but are clearly visible under a low power binocular. To begin with, the surface appears granulated owing to the continuous surface layer of sterrasters ; but in addition to these spicules there are long rhabds running, for the most part, longitudinally through the body and usually projecting well beyond. In every case these long spicules are broken and are either oxea or (more rarely ?) the broken shafts of large triaenes. Clearly they are not spicules made by the young *Geodia* in which they are embedded although, from their size and the appearance of the occasional cladomes of triaenes found, they could easily be the megascleres of adult specimens of *Geodia barretti*.

The next feature the young specimens have in common is that the surface

tends to be irregular. That is to say, even in the most regularly-shaped of them it is thrown into folds or grooves. This can be seen in some of the specimens figured, but is more marked than the photographs reveal. Finally, in practically every case, there are pseudopodium-like processes, clearly seen in such specimens as (Plate **1**, nos. 1, 60, 70 and 75) or smaller processes, seen only under the binocular microscope, as shown in text-figures 1–4.

Each specimen has been mounted and examined. All but a very few, which were mounted whole, have been cut into thin hand sections, and their examination shows that in the smaller specimens the tissues contain sterrasters only, apart from the large (obviously foreign) megascleres, together with a few of the smaller microscleres. The larger specimens, on the other hand, have in addition their proper oxea and triaenes which are becoming radially arranged. In some of the smallest of these the body is nothing more than a mass of sterrasters, with the smaller oxyspherasters scattered between them, held together with a loose

FIG. 1.—*Geodia barretti* : no. 44 (see Plate **1**, fig. 1) showing what appear to be several regenerative masses coalescing, with the ends of parental (?) spicules protruding.

tissue. Those slightly larger consist of an outer, cortical layer of sterrasters, with oxyspherasters as the only spicule in the inner tissues, and with the long, broken rhabds passing through. These last correspond closely to the specimen which Hansen (1885, p. 17) called *Geodia parva*.

The observations made on the structure of the skeleton and the details of size and form of the spicules, constitute all the evidence available as to the nature of these small sponges. There is, however, a considerable amount of speculative evidence, based on analogy, to suggest that they are young sponges (*i.e.* reproductive bodies) formed naturally from regenerative cell masses such as have been produced in the laboratory by Maas, Wilson, de Laubenfels and others. These experiments I have repeated and it is perhaps best to say here that the connection between the artificially-produced regenerative cell masses and the possible origin of the young *Geodia* was suggested by the appearance of such masses under laboratory conditions (**Plate 2**, fig. 1).

The normal method used in the production of regenerative cell masses is to place a piece of living sponge in bolting silk and, after twisting the corners of the silk together to form a bag, to squeeze the enclosed mass firmly. The pale milky fluid which emerges is allowed to drop into a glass dish of seawater. When first dissociated the cells are amoeboid. In course of time, however, the individual cells meet and coalesce, forming syncytia. These, in turn, move about and are joined by other cells, or other syncytia and fuse with them. In time the bottom of the dish bears a number of regenerative cell masses of varying sizes and shapes, which can be roughly grouped according to shape into (*a*) spherical or subspherical, (*b*) navicular or elongate, and (*c*) irregular. All show more or less pseudopodium-like processes at points along the margins

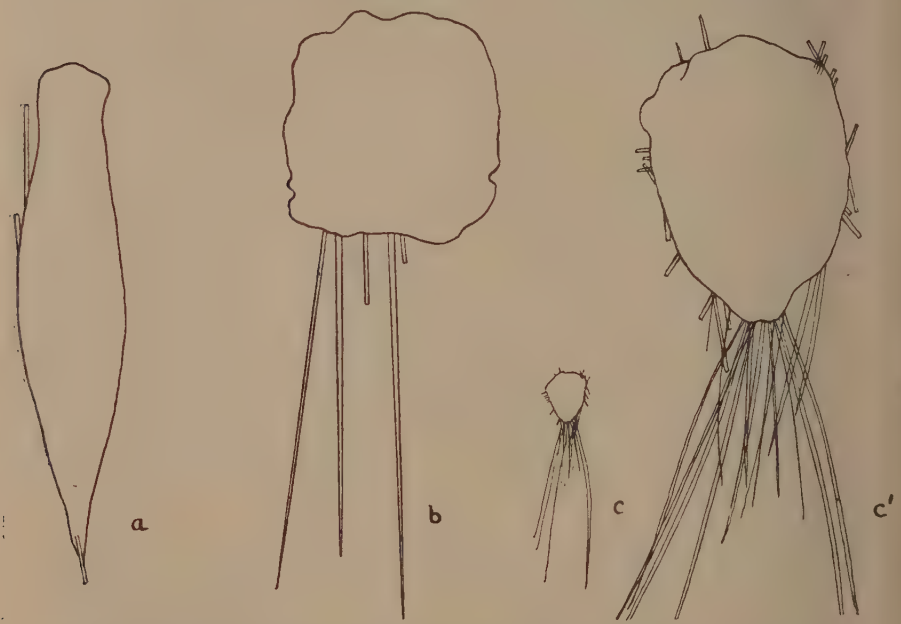

Fig. 2.—*Geodia barretti* : (*a*) no. 63 (Plate **1**, fig. 1) to show parental (?) spicules, ×20. (*b*), (*c*) and (*c'*) specimens from the bottom left hand corner of Plate **1**, fig. 2, to show the disposition of the parental (?) spicules. (*c*) and (*c'*) are drawings of the same specimens.) (*a*), (*b*) and (*c'*) ×12, (*c*) ×1½.

(Plate **2**, fig. 2). The spherical or subspherical masses probably represent something of a resting stage, the navicular or elongate represent the stage of active movement and the irregular represent the stage immediately following the fusion of one or more of the spherical or navicular masses. The photographs on Plate **2** show such regenerative cell masses.

The evidence including that already given for accepting these *Geodia* specimens as young sponges formed from regenerative cell masses, is :—

1. Their general form corresponds closely with that of the experimentally produced regenerative cell masses, and lacks the regularity of form associated with post-larvae produced by metamorphosis (in non-corticate sponges this is an incrustation of more or less rounded outline, in corticate forms it is spherical, but in both cases there is uniformity).

2. Although it is the case that adjacent post-larvae of the encrusting type will coalesce as their margins grow out towards each other and meet, there is a different appearance in the resulting masses, mainly no doubt because of the uniformity in shape of the component individuals.

3. The pseudopodium-like processes may occur on the margins of post-larvae derived by sexual reproduction but, judging from the available evidence it is a feature of the metamorphosis rather than a permanent feature of the post-larva. Moreover, such processes would be expected to be present in non-corticate sponges rather than in those which, like *Geodia*, have a stout cortex.

4. Had the young *Geodia* been derived from surface buds, as in the related *Tethya*, we should expect a greater uniformity in size and shape, and it is doubtful if coalescence of two or more would occur with the frequency seen in this case neither would there be the same irregularity in coalescing individuals (see Plates **1** & **2**).

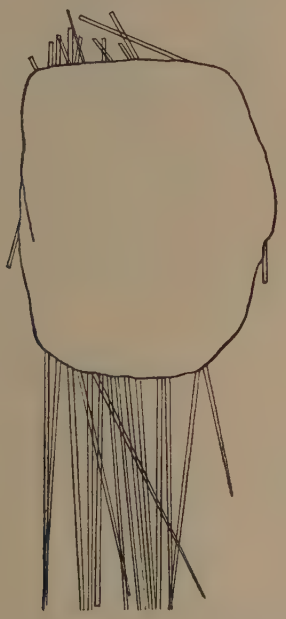

FIG. 3.—*Geodia barretti*: the top right hand specimen in Plate **1**, fig. 2, to show the disposition of what are presumed to be the parental spicules.

5. The presence of the foreign spicules could be due either to larvae having settled upon spicules lying free on the bed of the sea and, in the course of metamorphosis, having incorporated some of the spicules into their substance; or to the young sponges having been formed as buds on spicules protruding from the surface of the parent (as in *Tethya*) which were later detached; or as regenerative cell masses on the spicules either while projecting from the surface of the parent; or as regenerative cell masses on spicules lying free on the bed of the sea.

If the spicules were lying free on the bed of the sea then, whether the formation of the young sponges were by larvae metamorphosing or regenerative cell masses, we should expect such included spicules to be present in the base of the young specimen, instead of being scattered throughout the thickness of its body, even

to lying just within its surface all round the body. Apart from the fact that it is doubtful whether such a concentration of free spicules would occur as to give us the pattern shown, there is also a lack of erosion in the spicules themselves, and the absence of any marked quantities of other included materials, such as mud grains, organic debris, etc. On the other hand, the presence of foreign bodies (mud, etc.) in the surface layer but not in the interior suggests that the formation of these sponges was initiated while they were still attached to the surface of the

FIG. 4.—*Geodia barretti* : no. 13 (see Plate 1, fig. 1), showing what appear to be eight coalscent masses.

parent and that later growth took place on the sea-floor. This last point is further supported by the regular, bundle-like arrangement of the large, foreign (? parental) spicules usually along the long axis of the sponge (figs. 1–4).

6. There is no sign of larval spicules, such as should be looked for if the young individuals were the product of a normal larval sequence, or even if they had occurred as buds.

Having examined these small *Geodia* from the Arctic in the light of the knowledge summarized above, it may be said that they can hardly be derived from sexual or asexual ciliated larva because in all known cases among the Tetraxonida special larval spicules appear either in the embryo, the larva, or at latest at metamorphosis, which are recognizably distinct from the adult spicules. No such spicules were found in the specimens under examination. They differ, also, from all buds so far recorded in their irregular form, in all known cases the shape of the buds being spherical or subspherical, and, although a typical bud may contain parental spicules, it also possesses its own, usually smaller, spicules from an early stage in development. Finally, had the 100 *Geodia* been formed as a result of fragmentation the tissues must have contained spicules identical with those of the parent and represented by all categories of megascleres and microscleres. It is necessary, therefore, to postulate a new method of reproduction and the most logical suggestion is that the young *Geodia* have been formed by the natural production of regenerative cell masses. One possible means by which this may be effected is, as suggested here, in association with the extrusion of spicules.

Notes on the Arrangement and Development of the Spicules.

The arrangement of the skeleton and the categories of spicules comprising it vary much more than is usual from one specimen to another. The most marked features are the irregularity in the arrangement of the spicules and the apparent absence of correlation between the developmental sequence of the spicules and the size of the specimen. In fact, these very irregularities support the view tha the young *Geodia* have arisen, not from the metamorphosis of larvae, or even from buds, but from some more unusual process.

The method of examination was as follows : although a very few were mounted whole in Canada Balsam, the great majority were sliced with a razor longitudinally, giving for each specimen a series of sections as thin as it was possible to cut by this method. The sections were mounted in Canada Balsam, a separate slide being used for each specimen.

It was found that the individuals could be grouped according to the characters of the skeleton as follows :—

A. Specimen a solid mass of sterrasters, with oxyspherasters and oxyasters in addition ; without proper megascleres but with broken (parental ?) megascleres arranged more or less longitudinally.

Numbers : 3, 84

B. Specimen a solid mass of sterrasters, with oxyspherasters as the only other microscleres ; without proper megascleres and with broken (parental ?) megascleres arranged more or less longitudinally.

Numbers : 6, 8, 9, 11, 12, 13, 14, 17, 20, 23, 26, 28, 30, 31, 33, 35, 41, 42, 44 (pars), 45, 48, 49, 50, 51, 54, 55, 56, 60, 61, 62, 63, 64 (pars), 67, 68, 69, 70, 71, 72, 74, 75, 76, 77, 79, 83, 84, 88.

C. Specimen an almost solid mass of sterrasters, with a tendency to thin out internally ; with oxyspherasters and oxyasters in addition to the sterrasters ; megascleres, in addition to broken spicules, oxea and developing triaenes.

Number : 73.

C[1]. Similar to C, but with oxyspherasters only.

Numbers : 10, 32, 36, 44 (pars), 46, 52, 59.

D. Sterrasters arranged in a distinct, though thin, cortical layer, and with some sterrasters sparingly scattered in the choanosome ; with oxyspherasters and oxyasters as additional microscleres ; megascleres oxea and triaenes (ortho- and dichotriaenes) arranged radially.

Numbers : 1, 2, 18, 22, 80, 89.

D[1]. Similar to D but lacking oxyasters.

Numbers : 7, 13, 19, 29, 40, 57, 78, 85.

E. Similar to D but lacking orthotriaenes.

Numbers : 5, 34, 53, 86.

E¹. Similar to D¹ but lacking orthotriaenes.

Numbers : 39, 58.

F. Similar to D but lacking dichotriaenes.

Numbers : 24, 82.

F¹. Similar to D¹ but lacking dichotriaenes.

Numbers : 4, 5, 7, 15, 25, 27, 38, 44 (pars), 64, 65.

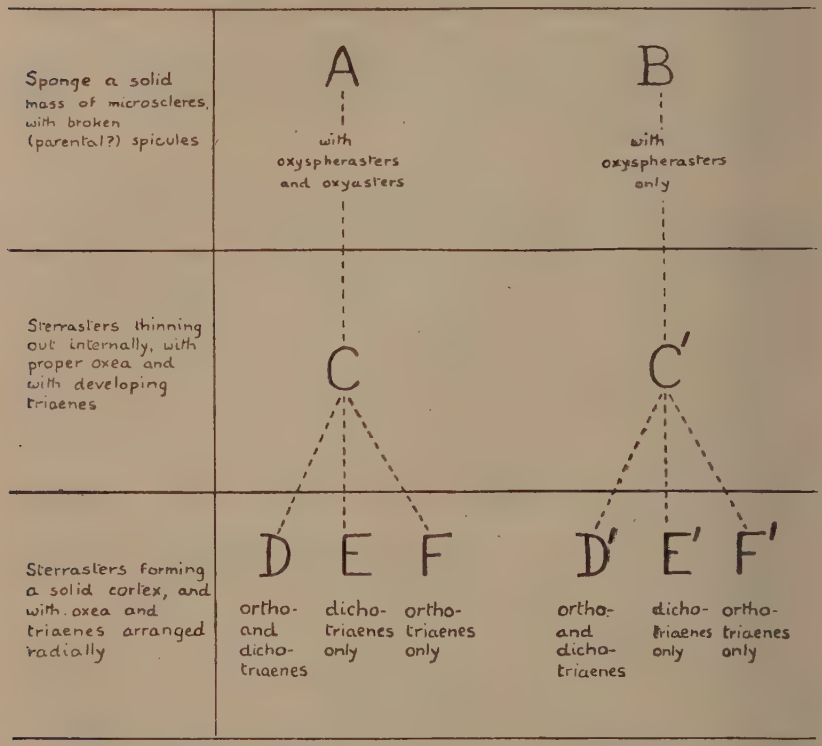

FIG. 5.—Diagram to show how simple variations in the microscleres and the cladi of the main triaenes, coupled with three successive growth phases, will combine to give 10 apparently well-marked groups. The characteristics of each of these 10 groups are of the order usually employed for specific differentiation, although they can be shown here to be obviously simple variants of a single pattern.

These groups are represented in fig. 5, which expresses their relation to each other from a developmental point of view. It should, however, be emphasized that although the symbols A to F represent stages in differentiation of the skeleton they do not show any correlation with the size of the individual. Thus, in group A, the least specialized, size ranges from that seen in 20 (the smallest in the collection) to 8, 13 and 74 (among the largest).

There are 10 distinct groups, based on a correlation between the spicules present and their arrangement in the skeleton, and these fall naturally into two

main lines, represented by A–F on the one hand and B–F^1 on the other. It could be argued that the two main lines represent separate species, or two varieties or even races of a single species, the distinguishing feature being the presence of oxyspheraster and oxyasters in the one and of oxyasters only in the other. These differences, small enough in themselves, are as great as those that have served in the past for varietal or even specific differentiation. In the same way, the different groups, based on the presence or absence of orthotriaenes or dichotriaenes, in addition to the characters of the microscleres, might equally represent 8 (or 10) species, varieties or races. Although the logic of such differentiation might be questioned, it cannot be denied that the action could be justified by analogy with species-criteria used by former authors. The strongest argument in favour of regarding all the young *Geodia* under discussion as conspecific is found in the characters exhibited by the various parts of specimens 13, 43, 44 and 64 (see figs. 1 & 4). Thus specimen 13, apparently the result of fusion between several individuals, can be aligned with groups A and D, according to which part of it is examined. In the same way, 43 can be referred to F^1 and A, 44 to A, C and F^1, and 64 to A and F^1. In fact, examination of these specimens suggests that the spiculation in this species of *Geodia* is more variable than has been thought hitherto, for it is most unlikely that individuals derived from parents belonging to different species, varieties or even races would fuse to form conglomerations such as are represented by 13, 43, 44 or 64. It has been shown that regenerative cell masses from cells of different species will not coalesce, and presumably the same holds true for varieties and races.

Variation in the spicules.—The variations in the skeleton may be summarized as follows :—

(i) The sterrasters seem to be the first spicules to appear, followed by the remaining microscleres.

(ii) Oxyspheraster arise first in 46 (group A) specimens as against the two (group B) specimens in which oxyasters appear first.

(iii) The oxyspheraster may, therefore, be regarded as the more primitive of the euasters, which would explain the rarity of their occurrence in older individuals.

(iv) As a rule the oxea, among the megascleres, appear next in order, although there is at least one specimen in which the triaenes appear first.

(v) Orthotriaenes and dichotriaenes may be present in the same individual, or individuals may have exclusively the one or the other. There are, in addition, those individuals in which the triaenes are orthotriaenes with a variable proportion of the ends of the cladi incipiently bifurcated.

(vi) Some individuals have mature orthotriaenes set in position with the cladi at the surface, but contain also developing triaenes at the centre of the body which are dichotriaenes. This, taken in conjunction with (v), suggests that in this species, at all events, these two triaenes are interchangeable forms (see *Periodicity in the production of spicules*).

(vii) The specimens with the most perfectly developed radial skeletons occasionally possess developing anatriaenes, suggesting that this spicule forms part of the adult complement.

(viii) The dimensions of the spicules in these small specimens are :— Oxea 1·0 to 1·6 by 0·02 to 0·032 mm ; orthotriaenes, cladi, 0·1 to 0·8 by 0·008 to 0·042 mm. ; dichotriaenes, cladi, 0·4 by 0·04 to 0·042 mm.; sterrasters, 0·08 to 0·12 mm. diameter ; oxyspheraster, 0·012 to 0·022 mm. diameter ; oxyasters, 0·02 to 0·06 mm. diameter.

Order of development of the spicules.—It is of interest to speculate whether the order of appearance of the spicules in a developing sponge bears any relation to the phylogeny. Unfortunately, the geological evidence offers little help in the matter. In the embryo arising from a fertilized ovum it is usual for the megascleres to appear first, followed by the microscleres. In the present specimens this order is reversed, the microscleres appearing first. The earliest stage found contains both sterrasters and one or other of the smaller microscleres. The order of appearance of the megascleres appears also to be fairly constant, the first being oxea which are developed much later than the

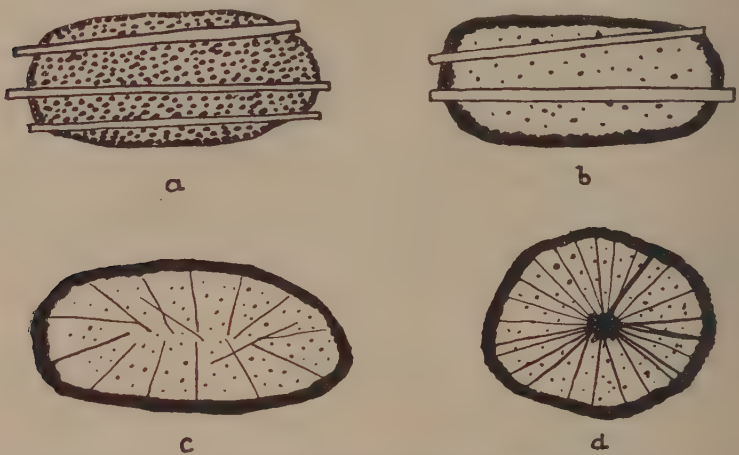

FIG. 6.—*Geodia barretti* : showing stages in the development of the skeleton :—
(*a*) Sterrasters uniformly scattered throughout the body, with foreign (parental ?) spicule fragments.
(*b*) Sterrasters forming a cortex (the foreign spicule fragments are still present).
(*c*) Oxea appearing.
(*d*) Radial skeleton complete.

microscleres. These are followed by the dichotriaenes or orthotriaenes and, at a much later stage, by a few anatriaenes. Protriaenes probably appear soon after the anatriaenes, but none has been seen in these specimens. It is possible that the presence of the broken (parental ?) megascleres tends to inhibit the formation of proper megascleres. At all events, it is noticeable that such fragments are sometimes included in the later stages of the developing skeleton, being moved from a longitudinal to a radial position as the sponge becomes rounded and develops its own radial megascleres.

Periodicity in the production of spicules.—In examining the numerous sections made during the course of the present investigations it became apparent that there is a pattern in the distribution, which is more emphasized in some sections than in others. In the early stages of growth the smaller microscleres are more or less evenly distributed throughout the tissues. From this stage there appears to be a migration towards the periphery. This is the normal method for all radial skeletons, noticeably in the Stellettidae and Geodiidae, where the developing megascleres can almost invariably be traced from the centre outwards. At or near the centre of the sponge are seen the undeveloped and, towards the periphery, the more fully-developed. A similar movement is seen in fig. 6 for the sterrasters.

Following the migration towards the periphery of the first euasters, it can sometimes be seen that the middle tissues are almost barren of this type of spicule but a fresh batch is appearing at the centre of the sponge (fig. 7). In extreme cases this leads to a banding effect. If the assumption is correct that spicules originate at the centre of the sponge, migrate towards the periphery and, later, are extruded ; and if it may be accepted that successive waves of spicules may vary in the characters of the component spicules, then some aspects of the spicule-variation are made clear. In the present case, it may be possible for the spiculation to include oxyspherasters and dichotriaenes at one stage, oxyspherasters and orthotriaenes at another, or any one of a wide range of permutations and combinations. In other words, the range of spicule-variation must be accepted as far wider than any writer, with the exception of Vosmaer (1932–33), who probably went too far in the opposite direction, has admitted.

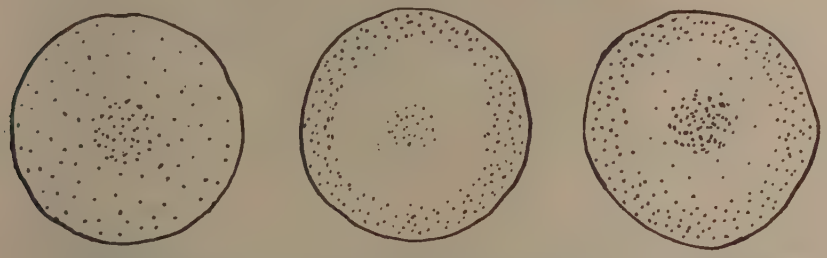

FIG. 7.—Cross sections of some of the young *Geodia barretti* to show the distribution of smaller microscleres only. (Diagrammatic.)
The distribution of the smaller microscleres varies from one specimen to another and the impression conveyed by a series of such specimens is of a periodic migration of the microscleres from the centre of the sponge.

A parallel case can be seen occasionally in the arrangement of the sterrasters and of the megascleres. Doubtless in time it may be possible to link this periodicity in the production of the spicules with their migration to and extrusion at the surface. In the meantime the possibilities opened up for the systematist are of considerable importance. For example, in at least one specimen the fully-developed triaenes in position at the periphery are dichotriaenes while the developmental forms at the centre, and in process of migration outwards, are all orthotriaenes. Similarly, in another series of specimens we have the following stages : (*a*) Choanosome filled with oxyspherasters distributed evenly ; (*b*) A layer of oxyspherasters at the periphery, with other oxyspherasters scattered sparingly in the choanosome, but with a mixture of oxyasters and oxyspher-asters at the centre apparently on the point of migrating towards the periphery.

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EXPLANATION OF THE PLATES.

Plate 1.

Fig. 1.—*Geodia barretti* : 89 of the specimens from the Arctic presumed to be formed from regenerative cell masses. ×2.

Fig. 2.—The rest of the specimens. ×2.

Plate 2.

Fig. 1.—Regenerative cell masses produced under laboratory conditions, to show the resemblance to the *Geodia* in Plate **1**, fig. 1.

Fig. 2.—A single regenerative cell mass highly magnified. (This is the specimen seen in Plate **2**, fig. 1 to the right hand border of the picture.)

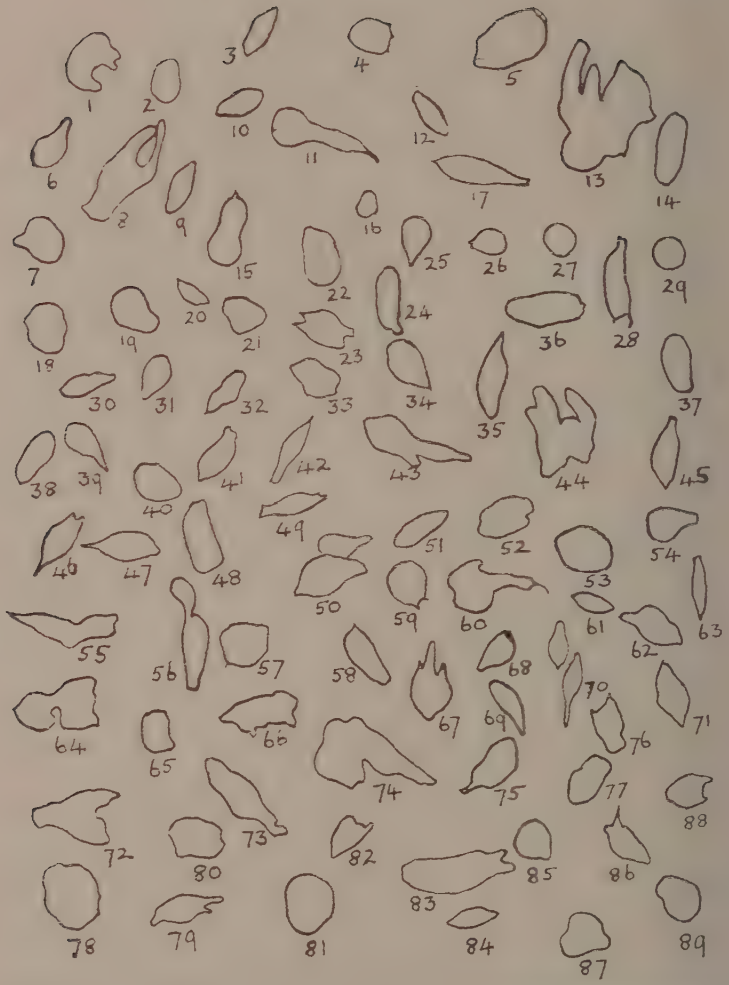
Plate 3.

Fig. 1.—A mature specimen of *Halichondria bowerbanki*.

Fig. 2.—A few of the supposed regenerating fragments of *Halichondria bowerbanki* found on the beach at Littlehampton. Their resemblance to fragments such as might be produced by the breaking up of the specimen shown in fig. 1 is obvious.

Fig. 3.—*Haliclona* sp. Growing on *Zostera*, showing the remains of the parent individual below, with the basal layer of gemmules exposed on the upper part of the leaf. ×$\frac{3}{2}$.

Fig. 4.—The same enlarged.



Outlines of the specimens shown in Plate 1, fig. 1, to indicate the numbers given to these specimens.

FIG. 1.

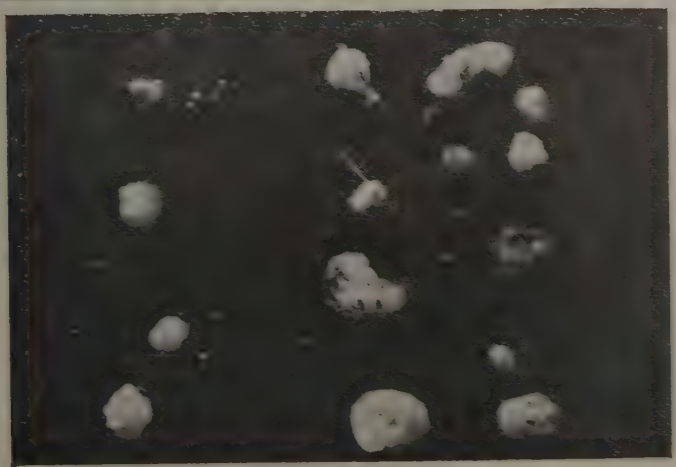


FIG. 2.

FIG 1.

FIG. 2.

Fig 1.

Fig. 2.

Fig. 3.

Fig. 4.

EDMUND DAVALL, F.L.S., AN UNWRITTEN ENGLISH CHAPTER IN THE HISTORY OF SWISS BOTANY.—FINAL ADDENDUM.

By G. R. de Beer, F.R.S., Pres. L.S.

The volume and the interest of the correspondence which I have received since the publication of my paper on Edmund Davall *, and the recent discoveries made by the Librarian in the Library of the Linnean Society relating to Davall, have combined to persuade me that this addition to my previous work may not be unwelcome.

Mr. Savage has been successful in finding in the library three items which belonged to Davall, and one which belonged to Wyttenbach ; all are of great importance from the point of view of the history of Swiss botany :—

(1) Davall's annotated copy of Haller's *Nomenclator ex Historia plantarum indigenarum Helvetiae excerptus auctore Alberto v. Haller.* Bernae, 1769. pp. [i]–iv, 1–216. 8vo.

Copy in which Linnaeus's binomials or specific epithets have been added in the margins throughout. Many of the species-numbers underlined, and some other annotations.

Pasted in at the beginning is a MS.—*Desiderata de Monsieur Chaillet de Neufchatel en Suisse.*

(2) Another copy marked by Smith on title-page : *ex dono opt. Davall*, 1790. On page 1, Davall has written, *R. In herbario* [Smith added :] *D. Reynier.* Davall has written *R* against many species up to page 192. The Fungi and Zoophyta (pp. 192–216) are not marked in any way.

(3) A copy of an earlier work of Haller, without a title-page, beginning : *Enumeratio stirpium quae in Helvetiae rariores proveniunt*, pp. 1–56.

Smith has written on the fly-leaf of this volume : *Ex dono Amiciss : Davall*, 1790. *J. E. Smith.*

Haller, Enum : Stirp : Helvet : rarior : libellus ineditus, rarissimus. [Another hand has written :] *1760.*

——*Nomenclator.—rarus liber* [another hand has written :] *1769.*

(4) A third copy of the 1769 *Nomenclator*, presented in 1925 by J. T. Jolley. This copy which had been previously in the possession of the Rev. Hilderic Friend has the book-plate of Robert James Shuttleworth †, which has been pasted over the signature of J. S. Wyttenbach. The Linnaean binomials or specific epithets have been added by Wyttenbach and another unknown writer.

Next, I wish to correct an error (to which my attention was kindly drawn by Dr. A. Becherer of the Conservatoire Botanique de Genève) in the legend to Plate **3**, fig. 2, in which I indicated *Fimbristylis dichotoma* as the modern synonym for Davall's name *Scirpus elongatus*. While this synonymy is probably correct for the reigning name *Scirpus elongatus* Poir. (*Encyc. Suppl.* v. 99, 1817), I had overlooked the fact that the name *Scirpus elongatus*, which Davall had had engraved under his figure in 1790, ranks as a manuscript name, since it was not published before I reproduced it on the plate in question in 1947.

It is clear from the correspondence between Davall and Sir James Edward Smith that this plant presented him with a problem to which he paid particularly close attention. In a ' Systematic List of plants sent to my friend Dr. Smith in the parcel of 28 February 1790 ', Davall included under No. 4, ' Scirpus supinus.

* *Proc. Linn. Soc. London*, **159**, 1947, pp. 42–65, and 140.

† R. J. Shuttleworth, 1810–1874 ; F.LS., 1856 ; English naturalist who lived at Berne from 1833 to 1866.

If I might dare alter sp. name should call it elongatus as it is not supinus here '. On this document Smith added in pencil : ' Those marked H are put into my Herb^{m} ', but no H has been put against No. 4.

On 30 March 1790, Smith replied to Davall and said : ' I think you may change the name of Scirpus supinus if certain that it is Linn^{s} plant, as I think. If not *quite* certain, call it S. elongatus and say an S. supinus Linn. ? ' Encouraged by this advice, Davall included his plant in the list which he sent to Smith on 29 June 1790, under the following description :—' VIII. Scirpus (elongatus) culmo tereti nudo, supra spicas sessiles glomeratas elongato, seminibus traverse rugosis.—N.B. to contrast with setaceus which has semina longitudinaliter *striata* '. Finally, Smith wrote to Davall, 11 July 1790, ' 4. Scirpus supinus, you may change to elongatus, giving your reason '.

The Smithian Herbarium contains the very specimen of the plant which served for Davall's figure. Attached to the sheet is a label in the writing of Du Cros : ' an Scirpus supinus Linei ? Videtur esse Hall. No. 1344 '. To this Davall added : ' Sic est. E.D. '. The specimen came to Smith with Davall's herbarium in 1802.

In the copy which Mr. Savage found (1, above) of Albrecht von Haller's *Nomenclator ex Historia plantarum indigenarum Helvetiae* (Bernae, 1769), in which Davall had entered in ink the Linnaean name opposite each of the plants enumerated by Haller ; opposite ' No. 1344, Mariscus folio gramineo . . . ', Davall wrote ' Scirpus elongatus N[obis]=supinus L. Sp. pl. '.

For the reasons given above, the name *Scirpus elongatus* cannot be given to this plant, which must be called *Schoenoplectus supinus* (L.) Palla (*Scirpus supinus* L.), according to Dr Edouard Thommen *.

Dr. Thommen kindly wrote to draw my attention to the interest attaching to Davall's inclusion of *Sonchus palustris* among the species discovered by him, either not mentioned by Haller or considered as doubtful natives. (Davall to W. Curtis, 12 Sept. 1787 ; *Proc. Linn. Soc.* **159**, 1947, page 140). This species, which is to-day lacking from the Swiss flora, was reported by Höpfner, ' entre Noville et Villeneuve ', and by L. Thomas and Gay at Viège, but these occurrences are regarded as doubtful.

The surest way to settle this problem would have been to find a specimen of *Sonchus palustris* with its locality in Davall's herbarium, which came to Smith in 1802, and much of which became included in the Smithian herbarium. The latter does not contain it, and the presumption is that when Smith received Davall's herbarium it did not contain it either. Between 1787 and his death in 1798, Davall must have come to the conclusion, either that he had made an erroneous identification or that the plant was not really a native. The puzzle is intensified by a statement that this plant grew in Davall's garden, without having been sown. It is in Reynier's *Mémoires pour servir à l'histoire physique et naturelle de la Suisse* (Lausanne, 1788). On page 213, among the list of plants found in Switzerland since the publication of Haller's works, is an entry for ' Sonchus palustris Linn. Dans les marais entre Noville and Villeneuve. J'ai lieu de croire qu'il croît aussi dans les marais entre Orbe and Yverdon ; puisqu'il a cru dans le jardin de M. Davall à Orbe, où il n'a jamais été semé '. The puzzle therefore remains.

In addition to the genus *Davallia* Sm., and the species *Gymnostomum Davalliana* Sm., Davall's name is commemorated in another plant, *Carex Davalliana*, concerning which Smith wrote as follows :—

' . . . CAREX *Davalliana*. *Prickly separate-headed Carex* . . .

' Specimens of this Carex were sent to me from Switzerland, as well as to Dr. Goodenough (see his postscript at the end of our 2d volume), by my much lamented friend the late Mr. Davall, who discovered it to be different from the Linnaean *dioica*, to which the synonym of Scheuchzer is referred in the *Species*

* *Atlas de poche de la flore Suisse*, Lausanne, 1945.

Plantarum. Linnaeus, however, has erased this quotation from his own copy of that work. Mr. Davall has assured me this plant is very common in almost every damp spot about Orbe; whereas he had met with the *dioica* only in one peat bog. I have no doubt of its being what Haller intended under his n. 1350; it agrees exactly with his description, though he has confounded under it synonyms of *dioica* and *pulicaris* at least, if of no more species. It appears to be the *dioica* described by Professor Wildenow in his recent treatise on the Carices found about Berlin, printed in the Transactions of the Academy of that place. Scheuchzer erroneously applied to it synonyms of Ray which belong to *C. pulicaris*, and has by that means been the cause of subsequent mistakes. Mr. Davall having first elucidated the subject, I have consecrated the specific name to his memory.' *

Dr. Bernard Gagnebin, Keeper of Manuscripts in the Library of Geneva, has very kindly informed me that under his care there are one letter from Davall to H. B. de Saussure (dated from Orbe, 1794), sixteen letters to Davall from the younger Albrecht von Haller (dated from Berne between 1790 and 1797), seven letters from Louis Jurine (dated from Geneva between 1787 and 1796), and one from Jean Senebier (dated from Geneva, 1793). With characteristic generosity Dr. Gagnebin has given me copies of some of this correspondence which, because of its great interest, and by kind permission of the Library of Geneva, I reproduce here.

The letter from Davall to de Saussure† is the answer to that which de Saussure sent to him saying that he would send him the lichens which he had collected on the Col du Géant (reproduced in *Proc. Linn. Soc.* **159**, 1947, p. 54). It forms the material on which de Saussure based the identification of the lichens in his book, and is itself, based on Smith's letter to Davall of 6 June 1794.

* 'Descriptions of five new British Species of Carex'. By James Edward Smith, M.D., F.R.S., F.L.S. (*Trans. Linn. Soc. Lond.* **5**, pp. 264–273, 1800, pp. 266–267).

† *Edmund Davall to Horace-Bénédict de Saussure.*

(Bibliothèque Publique et Universitaire de Genève, Dépôt de Saussure Ms. 82.)

'Orbe, 7 d'Octobre 1794

'C'est avec une peine réelle que je me suis trouvé obligé d'attendre si extrêmement longtems avant de pouvoir vous communiquer une réponse définitive au sujet des Lichens recueillis par vous dans votre très intéressant séjour au Col du Géant à 1760 toises au dessus du niveau de la mer et que je reçus de votre part en fevrier 1792.

'J'envoyai tous les exemplaires (n'ayant pas de double) en Angleterre à la fin de mai 1792 après avoir numéroté chaque morceau de "*Roche granitique ou Crystal de Roche*" et, au mois de juin suivant, lorsque j'eus l'avantage de vous voir chez vous et que vous me produisîtes vos exemplaires de réserve, nous y appliquâmes les numéros correspondans avec la note de mes propres conjectures, ce qui suffira j'espère pour l'application de ce que j'ai à vous communiquer actuellement à ce sujet.

'Soyez assuré que ce grand retard n'a nullement dépendu de moi. Le moyen le plus assuré d'avoir des renseignemens exacts au sujet de ces objets recueillis dans un site si infiniment intéressant étoit de les soumettre à l'inspection des personnes qui, par leur connoissance intimes des Collections originales de Dillenius et de Linnaeus sont mieux dans le cas de décider avec justesse que toutes autres dépourvues de ce grand avantage. Mais les personnes auxquelles je me suis adressé étant fort occupées, soit à leurs études soit au soin des ouvrages qu'elles ont mis au jour pendant cet intervalle, il a fallu nécessairement attendre le moment où elles ont pu y donner leur attention avec soin. J'ai enfin reçu les réponses suivantes du Dr. James Edward Smith, F.R.S., président de la Société Linnéenne de Londres et propriétaire des collections de Linnaeus, qui a examiné tous les objets que vous avez eu la bonté de me communiquer.—

No. 1. Lichen scutellis lividis. paroit être proche de L. Tartareus. L'exemplaire n'est pas assez complet pour décider positivement si c'est cela ou une espèce nouvelle.

No. 2. Lichen proboscideus L. et Lichen scaber Hudson } ensemble sur un morceau.

No. 3. Lichen scaber Huds.
— proboscideus L.
— fahlunensis L.
— geographicus L.

No. 4. Lichen geographicus L. [*Footnote cont. on* p. 182.]

Among the letters to Davall from the younger Haller, one of the most interesting is that of 10 March 1796, in which Haller proposes that Jean-Christophe Schleicher, of Bex, should make a botanical excursion at their joint expense, and asks him to choose from a couple of specimen itineraries which would take the collector through the regions at that time least well-known *. It is interesting to find that the practice followed by Joachim Burser for Caspar Bauhin, by Thomas Blaikie for Drs. Pitcairn and Fothergill, and by Huber, Gagnebin, the Thomas family and so many others for the great Haller, was still current at the end of the 18th century in Switzerland.

No. 5. Nova species., peut être nommée Lichen (tesselatus) crustaceus ater rimosus, tuberculis crustâ immersis planis angulosis lividâ. Smith mss.

No. 6. Lichen geographicus, proboscideus et pubescens.

No. 7. Dickson soupçonne que celui-ci peut être son Lichen. On ne voit rien qui ressemble à des . . . tella. C'est une très singulière production et probablement non décrite.

No. 8. Lichen geographicus L.
— mesenteriformis, Wulfen apud Jacquin misc. vol. 2, p. 85 ; Tab. 9, F. 5, et nova species quae dici potest :
Lichen (loricatus) crustaceus ater rimosus, tuberculis angulosis concaviusculis exiguis sub marginatis con coloribus nitidis.

Smith, mss.

' Je suis fort heureux d'aprendre de vous que vous n'étes pas trop mécontent de ce retard que j'aurois bien souhaité moins long. Je voudrois de tout mon coeur que ces remarques fussent encore assez à tems pour vous servir en traitant du Col du Géant dans votre 3me Vol. si impatiemment attendu et que j'ai appris indirectement que vous vous proposez de livrer à l'impression.

' Si vous pouviez me faire part de quelques uns de ces Lichens, surtout 1, 5, 7, et le dernier, je vous en aurois la plus réelle obligation comme je m'occupe à faire une collection aussi considérable qu'il m'est possible de ces végétaux. Agréez, je vous prie l'assurance de la considération distinguée qui vous est si bien dûe de la part de toutes les Personnes qui aiment et qui estiment les connoissances utiles à la société, et particulièrement de

' votre très humble et très obeissant serviteur '.

' E. Davall '.

*.... Je viens donc avec confiance et pour l'amour de la botanique vous dire que Mr. Schleicher, que vous connaissez m'écrit de Bex pour me presser de luy com[m]uniquer vos intentions relativement aux secours pecuniaires que vous voulez luy preter pour luy faciliter son voyage. Il me dit qu'il ne voudroit travailler que pour vous & pour moy & qu'il ne recevroit de secours que de nous deux. Je l'aideray de mon mieux, & luy fourniray en outre des adresses & des renseignemens sur la plupart des lieux, les passeports, & Voici les deux tournées que je propose. Veuillés avoir la bonté d'en choisir une, & de me respondre aussitôt, parceque le pauvre diable attend notre decision avec angoisse a Bex. Si vous pouvez lui ecrire en droiture, cela vaudroit presque mieux, parce qu'il seroit hors d'attente d'autant plustôt.

1re Route

Simplon
2. Journée Domo d'ossola
2. h. Crevola
6. h. Brugnone
6. h. Centovalle
Locarno
} Cette route traverse des montagnes assez hautes telles que le M. Generoso, et a peu pres de la hauteur et de la meme nature que M. Cenere. Elles sont incon[n]uës, et doivent etre interessantes.
4. h. Bellinzone de la par le M. Cenere a
6. h. Lugano
8. h. Gravidona
3. h. Chiavenna, de la par la
4. Journées Valteline a
Séjour de
8. Jours Bormio, de la par les Alpes Juliennes a
2. Jours Ponterasina dans l'Engadine, de la par le
2. Jours M. Albula aux Bains d'Alveneu, ou il y a le M. Teury
de la a Tusis ou a Coire selon la saison
de Tusis par le Bernardine a Bellinzone
Val Levantine
St. Gothard
Val de Bedretto
Obergestelen
Grimsel
Meyringuen
Berne.

N.B.—Dans cette route je prends pour point principal Bormio, et j'arrange tout pour qu'il y arrive aussitot que possible & qu'il en parte plus tard.

]*Footnote cont. on* p. 183.[

The copy of Haller's ' Nomenclator ' described above, in which Davall entered the Linnaean equivalents of the Hallerian names, is of interest for yet another reason, for it shows that Davall was in close relations with another contemporary Swiss botanist, Jean-Frédéric Chaillet (1747–1839) of Neuchâtel. Pasted on to the inside of the front cover of the book is a letter headed : ' Desiderata de Monsieur Chaillet de Neufchatel en Suisse ', which is followed by a list of 70 names bearing Hallerian numbers. Chaillet took to Botany on retiring from military service in 1791. He had served with the Swiss regiments in the French service, including Regiment Chateauvieux which mutinied at Nancy in 1790, and, as was the case with Lamarck, it was the flora of the Mediterranean where he was stationed that inspired him with a fervent interest in plants. Chaillet also paid to Botany the compliment of considering that its delights were more than adequate compensation for his deafness, for in 1791, Mme. de Charrière wrote : ' J'ai beau faire pour qu'il tâche de se guérir de sa surdité, ce que je crois très faisable : il est est si heureux, il est si passionné de sa botanique, il est si sage, si raisonnable, que ce n'est pas la peine pour lui que de se débarrasser d'une petite incommodité '. (*Madame de Charrière et ses amis*, P. Godet ; Genève, 1906.)

Chaillet was an indefatigable finder of new species, and de Candolle estimated at 148 the number of species of Cryptogams attributable to him*. It is therefore of considerable interest to find that Chaillet, at the outset of his botanical career, was in close relations with Davall.

Further information relating to Davall's family has come to me in letters from his great-granddaughter, Madame Mathilde Hager-Davall, of Aarau. The genealogical tree which I gave on page 61 (*Proc. Linn. Soc.* **159**), was described

2de Route

Simplon
Crevola
Brugnone
Centovalle
Locarno — excursion dans le Val Maggia
Bellinzone
Lugano — Séjour et une excursion sur le M. Generoso.
Gravedona
Chiavenna — de la une petite excursion au Campodolcino & Splugen, ou sur une autre montagne voisine et
Morbegno
Sondrio — excursion sur les montagnes voisines
Tirano
Bormio — Excursions sur le Braulio, Wormserjoch
Ponterasina — retour à Chiavenna par le Maloja
Splugen — de la par le Bernardin et
le Val de Misox a Bellinzone, de la
par le Val maggia dans le Vallais et en descendant le Valais
retour par la Gemmi
. . . .

Berne le 10. mars 1796 — A. Haller.

[Bibliothèque de Genève, Ms. Suppl.. 118.]

* ' Notice sur M. J. F. de Chaillet ' ; A. P. de Candolle, *Mém. Soc. Hist. Nat. de Neuchâtel*, 2, 1839.

Of the 148 new species found by Chaillet, 77 are listed by de Candolle in the *Flore française* (Synopsis ou le Supplément de la Flore, 1804–1815), in addition to 105 species previously imperfectly known ; 54 new species are given by M. Persoon in *Mycologia europae* (1822–1828), in addition to 67 species previously imperfectly known ; 18 new species are given by M. Fries in *Systema mycologicum* (1821–1832) in addition to 36 species previously imperfectly known ; 29 little-known species found in Switzerland are listed by Schaerer in *Lichenum helveticorum spicilegium* ; while J. Gaudin's *Flora Helvetica* (1823–1833) refers to *Cirsium Chailletii* (esp. controv.) *Scirpus Rothii*. His name is also commemorated in the genus *Chailletia* DC. (*Ann. Mus. hist. nat. Paris*, **17**, 1811, p. 153 and in the family Chailletiacées, R. Brown (*Bot. du Congo*, p. 23, DC., prod. **2**, p. 57).

as only tentative, and was incomplete in two respects. It omitted to indicate the existence of a *Mathilde Caroline Louise* (1824–1903), daughter of Edmond Davall (1793–1860), who married *Armand de Joffrey*, and left four daughters. One of these became Madame Dutoit, whose daughter-in-law, Madame E. Dutoit-Caloz of Corsier sur Vevey, very kindly showed me a number of family portraits. The tree also omitted to mention that *Emile-Frédéric-Henri-Edmond Davall* (whose dates should be 1834 (not 1835)–1896) married a second time, on 8 November 1875 *Elise-Friederike-Wilhelmine Hunziker*, and left two sons: *Edmond Davall* (1876–1919), and *Albert Davall* (1881–1915), and one daughter, *Mathilde-Elise-Augusta*, who married *Max Georg Hager*, and who has kindly supplied me with this information.

Madame Hager-Davall has also given some very interesting facts relating to Davall's forbears. She says that when she was young, her father used to tell her that her great-grandfather had sailed round the world with Captain Cook. This must have been the father of the botanist, Edmund Davall, who married Charlotte Thomasset, and was ' storekeeper of the navy slop-office ' at the time of his death in 1784.

I am further informed that M. Aimé C. Demole (a descendent of Mathilde de Joffrey-Davall) possesses a portrait of an Edmund Davall (born in 1690), painted in 1729 by a pupil of Hogarth. This portrait shows the subject in a red turban *, and the interest which it awakened in Davall's ancestry led to some discoveries which I was able to make through the kindness of the Society of Genealogists.

On December 8 1758, *Edmund Davall*, bachelor aged 21, of the parish of St. Lawrence Jewry, London, married *Charlotte Thomasset*, spinster aged 21, of St. Ann, Westminster. These were the botanist's father and mother, and this entry enables the dates of their births to be placed approximately in 1737.

On 17 March 1713–4, *Edmund Davall*, bachelor aged 24, of ' S. Gyles in the Feilds Mdx ', married *Sarah Lindsly*, spinster aged 22, of ' St. Andrew, Holbourne ', at Lincoln's Inn Chapel. This Edmund Davall must have been the botanist's grandfather whose portrait was painted in 1729. It will be noticed that Sarah Lindsly was of the parish in which the botanist was born.

It is probable that the ancestry of Davall can be carried back still further for two generations, the next being *Sir Thomas Davall*, who is described by Edward Hatton in his *New View of London* (1708) as the successor to *Thomas Davall* who died in 1660, aged 44, and was buried in St. Mary-at-Hill Church, and *Ann*, his wife, who died in 1700 aged 80.

On Davall's mother's side, the Thomasset family originated from Agiez, in the Pays de Vaud, in the 16th century. One member of the family died in Batavia in 1669, another fell in Napoleon's army during the retreat from Moscow. Yet another, was said to be established in 1930, in the neighbourhood of the Tower of London, in the wholesale greengrocery business, and to have been not unaware of his Vaudois descent. Davall's mother, as has been shown, was born about 1737, and her sister, the oldest aunt from whose card-parties Davall endured such agonies, died in 1793 aged 84, and was, therefore, born about 1716. Other members of the family, of whom Madame Dutoit-Caloz possesses portraits are, *Henriette-Julie Thomasset* (1759–1846), who married *Louis Daniel de Joffrey* in 1777, and her sister *Emma Thomasset* (1751–1813). I must also correct the mis-spelling of the maiden name of Davall's wife, which should read Crinsoz de Cottens. Her mother was *Louise-Marguerite Thomasset*. It may be of interest to add that Thomas Philip Dayrolles, son of Lord Chesterfield's Secretary, married a Mlle. H. G. Thomasset. And finally, to complete the network of interesting connexions of the family, Charlotte Tavel of Payerne, first wife of Emile Davall, was of the same family as George Frederick Tavell, Byron's tutor at Cambridge †.

* Information kindly supplied to me by M. Demole of Berne.

† Information kindly supplied to me by Professor H. Perrochon of Payerne.

LECTURES ON THE PRINCIPLES AND METHODS OF TAXONOMY.

In conjunction with the Systematics Association, the following Lectures were delivered to advanced University Students during the Session 1947–48. The Lectures were given in the Society's Meeting Room, with the exception of the first one, which, by courtesy of the Geological Society, was held there.

'General Principles', by Dr. A. Tindell Hopwood, Vice-Pres.L.S.

'Taxonomy in Vertebrate Palaeontology', by Prof. D. M. S. Watson, F.R.S.

'Taxonomy in Invertebrate Palaeontology', by Prof. H. L. Hawkins, F.R.S.

'Taxonomy in the Thallophytes, with special reference to the Fungi', by Miss E. M. Wakefield.

'Taxonomy in Seed-bearing Plants', by Dr. W. B. Turrill.

'Taxonomy in Invertebrate Zoology', by Dr. O. W. Richards.

'Taxonomy in Vertebrate Zoology', by Mr. H. W. Parker.

'Cytogenetics as applied to Taxonomy', by Prof. Irene Manton.

'Taxonomy as applied to Animal Ecology', by Capt. Cyril Diver, C.B.E.

'Statistics as applied to Taxonomy', by Dr. C. B. Williams.

'Taxonomy as applied to Plant Ecology', by Sir Edward Salisbury, C.B.E., F.R.S.

'Animal Genetics as applied to Taxonomy', by Dr. E. B. Ford, F.R.S.

OBITUARIES

The death of **George Herbert Pethybridge**, O.B.E., M.A., Ph.D., on 23 May 1948, removes one of the leading plant pathologists of the early part of the present century. He will always be remembered for his researches on potato diseases, his extreme thoroughness, his kindly nature, yet his open and fearless criticism of conclusions he felt to be unsound.

Pethybridge was a Cornishman, being born at Bodmin on 1 October 1871, and coming of a banking and legal family. He studied at University College, Aberstwyth and took an honours degree in Science at London University. Later he worked under G. Berthold at Göttingen. He had a short period as a science master at schools at Luton and Bath, an experience which he held to be most valuable to him in after life.

His long association with Ireland began in 1899 and continued till 1922. The Department of Agriculture and Technical Instruction was created in 1900 and Pethybridge was appointed Head of the Seeds and Plant Diseases Division. It was under that Department that he commenced, and carried out, researches on Ireland's staple crop, which made his name eminent and gave him a world-wide reputation. At first his investigations were undertaken in the laboratory at Dublin, but before long he agitated for and acquired what was an innovation at the time—a field-laboratory. This was situated in the heart of the ' seed ' potato area in the west of Ireland. Pethybridge had a flair for studying diseases in the open, noting the primary infections, tracing their origin, and following the spread and course of the disease throughout the entire year. It is not too much to say that the work carried out at the field-laboratory at Clifden revolutionized many ideas then current on several potato diseases. At this little laboratory, where the writer visited him in 1911, he worked entirely alone, but with the utmost enthusiasm, and maintained the highest scientific exactitude possible under the conditions obtaining. Later, when flax became an important crop, Pethybridge contributed several papers on the maladies of that plant. His most noteworthy purely scientific contribution was the discovery of amphigynous antheridia, which he first described for *Phytophthora erythroseptica*.

The researches of Quanjer in Holland had stimulated the study of virus diseases. At the first International Phytopathological Conference, held in America in 1919, much attention was given to this subject. Pethybridge, Quanjer and the writer attended as delegates from Europe. After the Conference proper the delegates visited research centres and also the principal potato ' seed ' growing areas in Canada and the States. The influence of climate on the intensity of the aphis infestation, as well as its effect in permitting progressively better yields from virus-infected crops as one travelled from south to north, struck Pethybridge forcibly. The conference and tour were of great value in orientating the research on virus diseases of the potato crop which was to be commenced shortly after in England, Scotland and Ireland.

Pethybridge possessed a truly scientific outlook. He was sympathetic towards systematics and had a good knowledge of the native flora. He assisted Lloyd Praeger in his ecological researches on the Irish flora and was responsible, with J. Adams, for the ' Census Catalogue of Irish Fungi '. He was President of the British Mycological Society in 1926. For 23 years he had been a Fellow of the Linnean Society, and it was only distance from London which kept him from regularly attending meetings. He was a member of the Royal Irish Academy and was honoured by the Royal Dublin Society in 1921 when it bestowed upon him the Boyle Medal.

In 1923, Pethybridge (having regretfully resigned his appointment in Ireland on the change of Government) was appointed Mycologist to the Ministry of Agriculture and Fisheries and Assistant Director of the Ministry's Phytopathological Laboratory at Harpenden. The heavy administrative duties connected

with the post left him little time for original work, but his previous experience in initiating fruitful lines of research were invaluable in enabling him to guide and develop the English Ministry's Phytopathological Service. He retired in 1936 and was awarded the O.B.E.

Pethybridge never married. He was a great lover of his country as well as of his science and always wished British research to be above reproach. He was fond of music, but his hobbies were few. He was a loyal and generous colleague, an excellent correspondent and greatly esteemed by the younger generation for his unfailing willingness to render them assistance. A. D. COTTON.

Herbert William Pugsley, who died at Wimbledon on 18 November last, was born at Bristol on 24 January 1868, and was proud to be a Devon man on his father's side. He was educated at the Bristol Grammar School and at the age of 17 came up to London where he studied privately for the Civil Service. In 1888 he was admitted to the Works Department of the Admiralty, in which he remained until a few years before his retirement in 1928, when he was in charge of the Admiralty Savings Bank. In the evenings he studied for his B.A. at London University, which he took in 1889. He married at 26, and his best wedding present was the Wimbledon house which became his home for the ensuing 53 years of his life. Only during the late war was he thrice forced to evacuate it on account of air-raids and flying-bombs. He was the father of six sons, three of whom survive him with their mother.

His first botanical publication was in 1900 when he contributed a short note to the *Journal of Botany* on the occurrence in the lake in Wimbledon Park of *Ranunculus Baudotii*, which was new to Surrey. This was succeeded by a long series of papers, short notes and county-lists which he contributed to the same Journal until its publication was suspended during the War, after which his last papers appeared in *The Naturalist* and the *Report and Transactions of the Devonshire Association*. His major works, however, were mostly published in the Linnean Society's Journal.

In 1902 came his first critical work, on the British Capreolate Fumitories. This was illustrated by his own drawings of the flowers and fruits of six species, and included the description of *Fumaria purpurea*, the new endemic species which had been confused with *F. Boraei* although it was much nearer *F. capreolata*. Two years later he described and illustrated the still finer Cornish endemic, *F. occidentalis*, first recognized by himself, and the clear style and critical methods of research which are characteristic of all his longer papers are completely in evidence in this early work. The Fumitories were his first love, they won and deserved his lasting affection, and in no other group did he attain such complete mastery: he became the world authority on *Fumaria* and its allies and would, no doubt, have been invited to write an account for Engler's 'Das Pflanzenreich' if the time had come for such an undertaking (Dr. Rendle, with his tiny monograph of the Naiadaceae, remained the sole British contributor). Pugsley's long paper 'The genus *Fumaria* in Britain', published as a Supplement to the *Journal of Botany* in 1912, with a page of his own line-drawings, was a splendid piece of work which still seems to many to be his best. It was the only paper in which he published anything approaching to a dichotomous key to the species; in all his other revisions the 'keys' take the form of a conspectus. It may be suggested that the reason for the popularity of this work is to be found in the plants themselves: the British Fumitories are for the most part clear-cut species of the first water, which need only patience and careful field observations for their understanding, although they become 'critical' in public herbaria on account of bad preservation and careless handling. Some years later Pugsley published a complete revision of the genera *Fumaria* and *Rupicapnos* in the *Journal of the Linnean Society*, and this was succeeded by a number of supplementary papers with descriptions of new species and records,

since collectors and botanists from all over the Mediterranean Region sent him their material for identification. In the same year (1919) appeared his first paper on *Euphrasia*, with the description of *E. confusa*, and in the following year he wrote a first paper on *Hieracium*, which was the result of twenty-five years' collecting.

Meanwhile, he had turned his attention to Narcissi, which he had been cultivating in his little garden for many years, having collected the bulbs on his holidays in the Swiss and Italian Alps. While preparing his paper '*Narcissus poeticus* and its allies' (*Journ. Bot.* 1915, Suppl.), he had his first experience of the old pre-Linnaean botanical literature, as it was necessary to go through the works of Parkinson, Gerard, Ray and later British writers, as well as those of the early Continental botanists, beginning with Lobel, Dodoens and Clusius. Many years later he did the same with the Daffodils: his monograph of '*Narcissus* subgenus *Ajax*' (*Journ. Roy. Hortic. Soc.* 58, 1933) is a very scholarly work of importance to gardeners as well as botanists and, no doubt as the result of his elucidation of these beautiful plants, he was awarded the William Herbert Medal of the American Amaryllis Society in 1940.

It is evident that Pugsley had been travelling far and wide during all these years in order to collect plants, particularly those of difficult groups. From an early age he had made a habit of visiting the Continent every year for part of his holidays. These visits were usually to the Alps, especially those of Switzerland, a country whose flora he came to know remarkably well, but there were others to France, Germany, Italy and Austria. He usually avoided the Mediterranean countries, of which he was suspicious on account of a digestion which had to be guarded, but in the spring of 1923 he visited Algeria with E. G. Baker and C. Norman in order to see the North African Fumitories and those curious brittle chasmophytes, the species of *Rupicapnos*, in their native home. In 1925 he was in the Eastern Pyrenees, with E. G. Baker and H. N. Dixon, while in 1930 he went by himself to collect Fumitories along the shores of Dalmatia and penetrated as far inland as the Bosnian capital, Sarajevo. A visit to the Channel Islands resulted in an important paper of critical notes published in 1914.

In 1928 Pugsley retired from the Admiralty. He was now sixty and was completely free to concentrate on more and more difficult groups of plants, at an age when many professional botanists are weary and disillusioned with the routine creation of new species and no longer feel the inclination to begin monographic work. His life from now on is an ascending scale of ceaseless and increasing activity, working up to a tremendous climax with his 'Prodromus of the British Hieracia'. In 1930 came his account of the genus *Euphrasia* in Britain, which was followed by many other papers on this group. Botanists abroad were induced to send him their specimens, and he wrote one paper on the 'Eyebrights of Iceland and the Faeroes', while his enumeration (1936) of the entire section *Semicalcaratae* landed him in the description of some new Asiatic species. But gradually he withdrew his interest from these difficult little plants, especially as he no longer had the surprising faculty of seeing their gland-tipped hairs without a lens. In 1935, a paper entitled 'On some Marsh Orchids' was a critical survey of the history and nomenclature of these plants and gave a synopsis of the British forms: Pugsley's sensational restoration (as he demonstrated) of the name *Orchis latifolia* L. to the plant which for so long had been called *O. incarnata* L. gained common currency among his countrymen but has not been accepted by several specialists on the Continent. There were a number of other papers on these Orchids, which greatly interested him, and *O. cruenta*, found by him at Zermatt in 1933, was new to the Alps. In Britain these plants hybridize freely with the Spotted Orchids, heterogeneous populations are common, while uniform hybrids sometimes occur in localities where the parents have died out: there was a risk that botanists in London might be describing new forms after brief visits to populations which were inadequately studied or from

specimens selected by distant correspondents. Another controversial revision, published like the last in the *Linnean Society's Journal*, was his paper on the 'British Robertsonian Saxifrages', which discussed the 'London Prides' and related Irish and Pyrenean species.

It was in that fruitful year, 1936, that Pugsley began to write the text of his last and most considerable work, the revision of those British Hawkweeds which he had been studying for so long. The difficulties encountered by him with the outbreak of the War are movingly described in one of the introductory sections of this work, the body of which was completed in 1943. At the moment of his death there was only some proof to be read, apart from the insertion of page figures in his huge index of specific names. The work has been published in the Linnean Society's Journal and its readers may well be astonished at the calm fulfilment under such terrible conditions of this task of extreme complexity. Few of them will have known that, when the air-raids on London began, he was advised by a friend to have a copy made of his manuscript for safe disposal. He had never before had his work typed and did not wish the manuscript to leave his hands at such a moment. He copied the whole of it himself: the final manuscript covered 432 pages of foolscap in his small neat handwriting and was sent direct to the printer. The work is beautifully illustrated by his own line-drawings of representative species of the main sections.

This brief sketch of his main work should be enough to reveal Pugsley as a notable European systematic botanist with an international reputation, and this fact should always be placed first in any estimate of his botanical career. But it is as the greatest British amateur botanist of our time that most of us think of him with affection and admiration, and it is probably as this that he would wish to be remembered. His chief interest from first to last was the study of the British flora and the gradual solution of the difficulties he encountered in it, and it is certain that his collecting trips abroad were largely undertaken with the object of improving his understanding of the plants of his own country. As he also travelled widely in all parts of the British Isles his knowledge and experience soon became unequalled, while for reference and study he had only to turn to his large private herbarium. Moreover, he lived in London and had the advantage of working in the great herbaria of Kew, the British Museum and the Linnean Society, of whose priceless libraries he made full and frequent use. His constant aim was to reduce chaotic groups to order, to give a correct name to anything he did not recognize, and to put errors right. And so, one by one, he attacked not only many of our more formidable genera, but also a long series of problems in smaller groups which were interesting or difficult for various reasons, such as *Hypericum*, *Jasione*, *Orobanche*, *Salvia*, *Gentiana*, *Herniaria* and *Juncus*, to name only a few. At the time of his death he had a written list of a large number of British species, each of which could provide him with material for one of his critical papers.

Although, as he often insisted, he did not go out of his way to see our rare plants in their famous localities, he was like all of us in his wish to find something new, and he did not despise the vice-comital lists of records which were once a familiar feature of the pages of the *Journal of Botany*. In fact, two of his early papers were elaborate studies of the flora of the Wimbledon neighbourhood which were published locally; while his 'Flora of Combe Martin', where he spent his last period of evacuation from London, appeared at the time of his death. His own additions to our flora were remarkable. Apart from the new critical species which he described, he was the first to recognize his *Fumaria occidentalis*; the discoverer of *Calamintha baetica* at Corfe in 1900; of his *Limonium transwallianum* and of *Gentiana uliginosa*, on a summer holiday at Tenby in 1924; of *Spergula vernalis* in East Sussex, during one of his periods of evacuation in 1943; and of a large number of varieties, the most interesting of which was *Myriophyllum alterniflorum* var. *americanum*, an addition to the North American

element in the Irish flora and described by himself as new. He also rediscovered *Carex depauperata* in its North Somerset station, and added *Sorbus porrigens* to the flora of Ireland. His second new species of Sea Lavender, *L. paradoxum*, from St. David's and Malin Head, which was not his own discovery but greatly excited him, needs further study and cultivation. The peculiar flower heads may prove to have less morphological significance than he believed, and his own words, 'the salient feature . . . is the abnormal inflorescence', may be found to be only too true.

As Pugsley came into prominence as a botanist of exceptional ability and strong character, it was natural that some tension should arise between him and G. C. Druce, who was the doyen of British systematists and enjoyed an enormous reputation as controller of the 'Botanical Society and Exchange Club of the British Isles'. They clashed swords over the interpretation of Clary, when Pugsley reduced Druce's *Salvia Marquandii* of the Channel Islands to the Linnaean *S. Verbenaca*; and again over *Calamintha baetica*, which Druce sought to treat as a variety of the Common Calamint, less by sound taxonomic argument than by mis-statements and false citations which were careless rather than intentional. And there was one famous occasion in August 1930, when the two men were accidently thrown together (by Druce's unexpected arrival) as the guests of Mr. and Mrs. Foggitt at Thirsk. The party made an expedition to Teesdale and *Juncus alpinus* was found by Pugsley at Winch Bridge and was later claimed by him as a first record for England. Druce then pointed out that he had known the plant in Teesdale since 1903, and referred to a MS. note by F. A. Lees in the latter's copy of the 'List of British Plants'; he also wrote that the plant was not *alpinus* but the Scandinavian *J. nodulosus* Wahlenb. Pugsley contested this identification, which was certainly wrong, but Druce may have derived a little comfort from the elaborate paper (1931) by the Swedish botanist Lindquist, who reduced Pugsley's newly described *J. Marshallii* to varietal status under *J. alpinus* and admitted *J. nodulosus* to the British flora on the evidence of a single Scottish gathering from Blair Atholl. In spite of all this, there was really no question of the two men being rivals, much less enemies. They were of strong but wholly different character, and their main interests could not collide. Pugsley knew that posterity would judge their contributions to pure science and, though far more of an *homme fait* than many botanists, he had not the social, indeed the cosmopolitan, outlook of Druce, whom he recognized without envy as a man of the world. Eventually it fell to Pugsley to write the obituary notice of Druce for the *Journal of Botany*, and a re-reading confirms one's impression of the extraordinary fairness of his estimate, while in the last sentence he indicated what so many of us knew, that Druce was a great humanist as well as a most distinguished botanist.

In later years, after Druce's death, Pugsley towered like an Everest above contemporary amateur systematists. Most of them had not travelled enough, or had too little experience of how to work in big herbaria and libraries; on the whole, they were men of altogether different calibre. But there were two, H. N. Dixon and W. C. Barton, of whom he always spoke with great respect; and he was pleased to remark the appearance of a number of young hopefuls, from whom he was separated by age-groups strangely destitute of botanists. His own success and pre-eminence were due to a fortunate combination of qualities and circumstances. He was endowed with exceptional intellectual gifts, foremost among them the natural aptitude of a scholar for minute research, and the power of clear and logical thinking. He took nothing on trust, checking and weighing every reference and statement with indefatigable industry and accuracy, conscious of his own great ability and believing in himself completely. Added to this was a tireless concentration of purpose and effort. He was undisturbed by all those external stimuli and incitements to competitive pleasure which are the ruin to-day of creative work in so many minds and wills.

In fact, he was always making the best of his great gifts, and was deriving pleasure and happiness from doing so. This was made possible by his residence in London and, chiefly perhaps, by the wife who not only looked after the home and brought up the boys, but also saw to it that nothing should stand in the way of her husband's work and travels, and was always a sympathetic listener to the stories of his adventures or skirmishes with other botanists.

Of course, Pugsley was a great individualist. Anything in the nature of ' joint work ' would have been as inconceivable to him as it was abhorrent to Bentham, and he never submitted specimens to other botanists for identification. On the other hand, he was always ready to help others, he was a referee of both exchange clubs for many years, and was constantly receiving parcels of specimens of the many critical groups of which he was master, in this way maintaining his position and preventing those groups from lapsing once more into chaos. His independence and self-reliance were revealed even in his method of travel : everything, even botanical equipment, was packed in two suitcases which he could carry himself, avoiding the porters at the Paris termini. He was very suspicious of interference with or mis-representation of his work by careless editors or writers, and it was obvious that he had suffered from such handling in the past, beginning with the occasion of his publication of *Fumaria occidentalis*, when at least three botanists came across him on account of carelessly expressed or foolish comments in print. He was quick to answer any published criticism of his work, and the possibility that a name might have to be altered or transferred owing to the complex vagaries of the International Rules of Plant Nomenclature gave him a particular dislike of the phrase ' comb. nov.', which, he pointed out, could not be found in those Rules. The suspicion that others might steal the credit that belonged to him led him sometimes to look for motives which did not exist, and he did not make enough allowance for the frailty of slipshod minds and pens.

He had a wonderful eye for plants, but his intuitions were always based on past experience and were then submitted to all the methods of the trained systematist. And so, although he detected and described many microspecies and minute varieties and forms, a Pugsley plant *differentia* was phenotypically a valid one when tested by other eyes, whatever value might afterwards be given to it by the fluctuating judgments of ' omega ' taxonomists. Above all, he never rushed into print. It has been made clear earlier on in this notice that his monographic work was usually the fruit of at least a quarter of a century of field observations, cultivation and literary research, a fact which may be commended to the attention of those who are encouraging beginners to undertake taxonomic studies. When he did commit his ideas to paper the argument proceeded with inevitable logic in his pleasant rhythmical English style, which avoided all pretentious jargon and nebulous speculation.

His work at home was done in a small room, facing north, in which everything was in perfect order. I never saw a dissecting microscope there, and he did not possess many books. Those he had were current manuals, monographs and floras, and two which earned his constant praise were Rogers' ' Handbook of British Rubi ' and Gremli's ' Flora of Switzerland '. The herbarium did not take up much space because he did not mount his specimens, except those of avourite groups, but kept them fully labelled in newspaper folders, a practice which released him from much of the mechanical side of herbarium work. By the terms of his will it is bequeathed to the Herbarium of the British Museum (Natural History), with the stipulation that representative specimens of the new groups described by himself should be allotted to the herbaria of Kew, the South London Botanical Institute and two foreign institutions *.

At a first meeting Pugsley seemed a little formidable. He had the appearance of a savant, dressed carefully, and walked slowly and with dignity. He approached even friends with a cautious, almost suspicious, look in his shrewd,

* The Universities of Zürich and Algiers.

penetrating eyes. But this quickly changed into a whimsical smile and a most affable manner with those whom he liked and trusted. His was a most kind and gentle nature, and as he was sociable and a great talker he was excellent company for his many botanical friends, although like all real botanists he was often alone on his plant-hunting expeditions. He rarely addressed meetings, and lecturing was a form of expression for which he felt no need ; his voice, indeed, was an instrument not well adapted for that purpose. But he was eager to meet and help botanists of all ages, although he disliked cocksureness in the young, especially when it was backed by neither experience nor knowledge. He was a close observer of his fellow-men, by whom he was determined not to be outwitted : their foibles and mannerisms appealed to his sense of the ludicrous, and without malice he could mimic some of their eccentricities, while his closer friends knew that he was also a writer of comic verses and composed maxims in the manner, as he said, of La Rochefoucauld. He lived very simply but, in spite of his regular habits of hard work and a regime of three meals a day, there was an endearing streak of civilized hedonism in his careful choice and appreciation of food and other comforts, and in his love of travel and natural beauty. He never needed the wireless, the cinema or most other mechanical pleasures, but as he grew older he much enjoyed expeditions in the cars of his friends, and on such occasions he kept up an incessant flow of gossip, by no means only on botanical matters, to the delight of his driver.

No one of our time showed a greater, more single-minded devotion to botanical study, but he cannot be called one-sided. Those long and intricate papers on historic European plants could not have been written without a wide general culture, a knowledge of languages, and a feeling for history and literature. During his enforced war-time stay in Devonshire, where he was without books or specimens, his active mind turned to the history of the neighbourhood as well as to its botany, and he wrote a paper on the antiquities of Lynton and Lynmouth. And he had a second great interest, the collection of water-colours. He attended the London sales regularly, and at the end of his life there were seven or eight hundred paintings which covered the walls of his house or were kept in portfolios. These were mostly of the English school of the nineteenth century and make no appeal to contemporary taste. He himself had no use for modern movements in art, of which he said, ' They can't draw, and are trying to conceal the emptiness of their minds '.

When the second Great War came Pugsley was deeply disturbed, but he did not share the faith of crusading idealists. He had given and lost his eldest boy Charles, a promising naturalist with whom he had collected butterflies (commemorated in *Fumaria Caroliana*), in the previous one, and now he was critical and suspicious of Anglo-Saxon motives. Whatever might be true of the Nazi rulers, he had a profound admiration for the German people and their industrious habits, which resembled his own and of which he saw all too few signs among his countrymen—' The English don't want to work ' was a favourite phrase. Though liberal by temperament as well as in politics, he was concerned at the changing character of English life and the attitude to work, as revealed by one habit he particularly disliked, the increasing custom of ' elevenses ', which was all right for factory hands but incomprehensible in professional establishments where the staff might be expected to be concentrating on interesting work. As he watched the rapid collapse of the standards and values of the Pax Britannica he was glad that he would not live to see the new order, in which he believed that many of the good things he had known would be absent and forgotten. Meanwhile, amid the general *malaise*, in spite of much frustration and discomfort, he would continue and complete his work on British Hawkweeds.

Pugsley was elected a Fellow of the Linnean Society in May 1920, withdrew from Fellowship in May 1940, and was re-elected in May 1947. No plant of high rank bears his name : it is found only in *Fumaria Schrammii* Vel. var.

Pugsleyana Maire ex Pugsl. Surely there is some new genus or species, perhaps a tropical orchid of outstanding beauty and distinction, unlikely to be reduced or transferred, which can be chosen to commemorate this life of devoted labour and great achievement? N. Y. SANDWITH.

James Lawrence Chaworth-Musters died unexpectedly on 12 April 1948, at the age of 46. He was apparently in good health, and in the best of spirits, and filled with enthusiasm for what he referred to as his ' magnum opus '.

He was the youngest son of the late Mr. and Mrs. J. P. Chaworth-Musters of Annesley Park, Nottinghamshire. After leaving his private school near Hertford he went to Rugby. Here he was never very keen on games though he became a good cross-country runner and, in later life, a very good shot with both gun and rifle. His chief out-of-school activity was the study of natural history in the field.

After leaving Rugby he went up to Cambridge, to Caius College, where he first of all began to read medicine but later gave up the idea of becoming a doctor and read geography instead. This latter subject remained an interest of his for life and he was an active and enthusiastic Fellow of the Royal Geographical Society.

As a young man he inherited from his father a mountain estate on the west coast of Norway, near Surendal, and here for many years he spent the summer months, making field studies of mammals and birds.

His main interest in life was the systematics of mammals and, except for the war period, he was for the last twenty years a regular worker in the Mammal Room of the British Museum (Natural History). As a systematist his knowledge was deep and his critical judgment extremely sound. He belonged to the ' lumpers ', as indeed do all good modern workers, and all his work was directed in an uncompromising manner to defining the species. The genera and subspecies interested him not a bit—it was the fundamental thing, the real thing, the species.

He published very little, unfortunately. This was due in part to a restlessness which made him intolerant of paper work ; he had the details of his subject in his head and it was merely a bore to write them down when he could be better occupied in new research. But perhaps it was due chiefly to a passion for truth and a feeling that once a thing is published it cannot be retrieved. The thing had to be exact and perfect before being committed to print. There is much to be said for this outlook and if the badly served fare of some workers had been more carefully prepared the systematist of today would not be suffering from such indigestion. But he took far too modest a view of himself and it is a great pity that he did not publish more. His ' magnum opus ' was a checklist of the Palaearctic mammals, for which he has left a great deal of manuscript. Apart from the systematic interest of the work, its publication will prove of great value on account of the remarkably erudite research on type localities which he put into it. There will be some difficulty with his handwriting which was paradoxical in being at the same time very neat yet almost illegible.

He made various expeditions in order to solve certain problems in connection with his work and these took him at various times to Jan Mayen Land, Cyrenaica, Greece, Russia, Morocco and Afghanistan. He was a very successful collector of birds and mammals and his study skins, of mammals at all events, are among the best in the Museum.

At the outbreak of war in 1939 he was working at the British Consulate in Bergen and when the Germans invaded Norway he left hurriedly, travelling eastward across the mountain on ski. The invading forces on the east cut him off and forced him to retrace his steps. Eventually he reached the coast and persuaded a fisherman to take him to the Shetlands and brought with him two British soldiers who had been in hiding in a nearby village. On his return to England he offered his services to the War Office and was shortly afterwards

commissioned as a Lieutenant (Special Branch) R.N.V.R., and in this capacity worked with a special service unit of the Royal Norwegian Forces. For this work he received the Norwegian War Medal.

As a man he was in many ways a paradox. In personal appearance he was Bohemian and disregarded many conventions, yet with it all he was at heart a country squire and a strong traditionalist. In spite of his usual dress there was, in its leather case in his room at the Museum, a top hat, ready for use on formal occasions. And the narrow, plainly knitted strips of material which he habitually wore as ties were not, as might have been imagined, badges of his unconventionality. They were what schoolboys of his day wore ; he was used to them and he liked them and he still wore them. And they were in a way the key to his character, for he was very much a schoolboy in his heart. He would fly all sorts of conversational kites which would lead casual, or pompous, acquaintances to think him a bit eccentric, or even a bit of a fool. How mistaken they were, and what very good value his company was to the discerning.

Perhaps the most delightful feature of his character was that he knew no evil. It was not merely that he was a good man. He simply did not know about unkindness, envy, greed, etc. Which was the chief reason why everyone in the Museum liked him and why, quite apart from his technical knowledge, he will be greatly missed, especially by his colleagues in the Mammal Room.

T. C. S. MORRISON-SCOTT.

ADDITIONS AND DONATIONS TO THE LIBRARY 1947-48

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INDEX

[A star * denotes the first publication of a name. Synonyms are not included.]

ACCOUNTS
1947–48 159
AUDITORS 57, 73
ACOCEPHALUS
nervosus (Schrk.) 27
ADENIA
lobata 151
ADMISSION OF FELLOWS
Abbis, Capt. H. W. 153
Andrews, C. E. A. 38
Balfour, A. P. 153
Barnard, T. T. 39
Bayne, Miss K. M. 153
Bell, P. R. 1
Blake, A. E. 153
Blakelock, R. A. 153
Blount, B. K. 2
Bradshaw-Bond, M. 1
Bullock, A. A. 153
Chew, C. W. 153
Cork, Flt.-Lieut. A. J. 1
de Worms, C. G. M. 85
Duddington, C. L. 84
Duerden, H. 1
Dunkley, H. L. 39
Edwards, F. 2
Fairbairn, J. W. 1
Ford, P. 153
Fraser, W. S. 153
Graham, R. A. H. 1
Greenshields, F. 48
Gregor, Rev. A. G. 153
Gregory, P. H. 153
Harding, J. P. 85
Harrison, R. J. 84
James, W. Warwick 39
Kennedy, G. Y. 74
Khan, A. S. 84
Kramer, L. M. J. 38
Lambert, Miss J. M. 1
Langham, H. G. 85
Lewis, Miss P. 153
Lloyd, L. C. 38
Marshall, H. S. A. 153
Matthews, L. Harrison 57
Montgomery, W. E. 38
Nash-Wortham, J. R. H. 153
Nelmes, E. 153
Newth, D. R. 153
Newton, R. G. 85
Peterken, J. H. G. 85
Pichi-Sermolli, R. E. G. 153
Prestwich, A. A. 85
Puri, G. S. 48
Santapau, Rev. H. 1
Stephenson, N. G. 153
Thornton, H. G. 153
Townsend, C. C. 38
Underhill, R. M. 47
Walker, F. T. 1
ADMISSION OF FELLOWS (*cont.*)
White, Miss K. M. 1
Wiehe, P. O. 85
Wilkinson, J. 1
ADOCIA
cinera 166
AEGIPHILA
alata 134
AGRIOCHOERUS 79
AGROMYZID 19
ALEBRA
albostriella (Fall.) 19, 32
ALGAE
drawings of Blue Green 51
parasitic Red 52
AMAZONIA
Psychotriae Theiss. 130
Sideroxyli * Hansf. 128
sp. 124
AMBLYTYLUS
affinis Fieb. 35
AMENTIFERAE 46
ANACARDIUM
occidentale 127
ANGIOSPERMS 42
ANDRENA
gwynana K. 29
ANISOPTERA
thurifera 139, 147
ANOPLIUS
fuscus (L.) 18, 19, 22
nigerrimus (Scop.) 22
ANTHOMYIA
sp. 18
APHELINUS 32
APHRODES
bicinctus (Schrk.) 28
ARANEA
redi Scop. 22
diadema L. 22
foliata Fourcr. 22
ARBER, A.
Linnean Medal 47, 154
ARCHAEOHIPPUS 79
ARCTOSA
perita (Latr.) 14, 20, 21
ARMATELLA
Litseae Syd. 151
Yatesii * Hansf. 151
ARTHROBOTRYUM
sp. 134
ASCAPHUS 56
ASSISTANT SECRETARY
Report 155
ASSOCIATES ELECTED
Wanstall, P. J. 75
ASTERINA
Acalyphae Syd. 142
anisoptericola * Hansf. 142
Anisopterae Syd. 147

ASTERINA (*cont.*)
asperulispora Gaill. 143
Aucubae P. Henn. 143
Cassiae Syd. 143
Champereiae * Hansf. 149
consobrina Syd. 150
crotonicola Pat. 149
Dictylomae P. Henn. 144
diplopoda Syd. 144.
Gmelinae Sacc. 145
grammocarpa Syd. 128, 145
indecora Syd. 121
Lawsoniae P. Henn. and P. Nym. 145
laxiuscula Syd. 128, 146
Litseae Yates 146
melanomera Syd. 146
perpusilla Syd. 121
Phoebes 136
Pipturi Syd. 125
rizalensis * Hansf. 147
Schmideliae Gaill. 147
singaporensis 147, 148
submegas * Hansf. 148
trachycarpa Syd. 148
Turnerae P. Henn. 148
Zizyphiae Yates 126
ASTEROLIBERTIA
Anisopterae * Hansf. 139
Bakeri * Hansf. 139
gibbosa * Hansf. 141
Licaniae * Hansf. 140
licaniicola * Hansf. 140
nodulosa * Hansf. 141
Ulei * Hansf. 142
AUDITORS 57, 73
Alston, A. H. G.
Burkill, I. H.
Parker, H. W.
Turrill, W. B.
Wakefield, E. M.
AUCUBA
japonica 143

BARBACENNIA
purpurea 136
BARNES, B.
on Ranunculus Flammula Linn. 74
BASUTOLAND PLANTS
drawings 49
BELLAIRS, A. d'A. and HAINES, R. WHEELER
on brain-case of tetrapods 40
BENEFACTIONS 197
BERIS
chalybeata (Forst.) 31
BERMATISTES
sp. 50
BIDENS
squarrosa 131
BIGNONIA
capseolaris 133
capreolata 133
BIRD MIGRATION and HOMING—DISCUSSION 85
Speakers :—
Fisher, J. 112
Newton, R. G. 114
Pirenne, M. H. 113, 116
President 85
Speakers (*cont.*) :—
Thomson, A. Landsborough 108
Thorpe, W. H. 84, 115
Tucker, B. W. 111
Wilkinson, D. H. 94
Wynne-Edwards, V. C. 110
Wojtusiak, R. J. 99
BIRDS
orientation 85, 94, 99
BLEPHAERIPUS
leucostomus (L.) 32
BOAS and PYTHONS
life history of (film) 163
BOBART, J.
book herbarium 55
BRAIN-CASE
of Tetrapods 40
BRISTOWE, W. S.
on British Hunting Wasps 3, 12
BRUMEA
Meyeri 138
BULIMUS 76
BURKILL, I. H.
on Tamus communis Linn. 39
BURTON, M.
on sponge Geodia barretti 2, 163

CAESALPINIA
nuga 124
CALAMUS
sp. 140
CALLICARPA
Blancoi 134
CALLIPHORA
erythrocephala Mg. 27
sp. 19
CAMPBELL, J. W. and CAMPBELL, M. S.
on Survey of Outer Hebrides 57
CANARIUM
sp. 152
CANIDIELLA 36
CAPSUS
meriopterus (Scop.) 35
CASSIA
Kirkii 151
quinquadrangulata 123
CERATODUS 82
CERCERIS
rybyensis (L.) 13, 19, 28, 34
CEROPALES
maculata (F.) 21
CERTIFICATES OF RECOMMENDATION
read 73
CHAMPEREIA
Cumingiana 149
CHLOROPISCA
circumdata (Mg.) 33
notata (Mg.) 33
CHLOROPS
calceata Mg. 33
sp. 19
CHORTOPHILA
cilicrura Rdi. (florilega Karl) 27
sp. 31
CHRYSIS
cyanea (L.) 24
viridula L. 37
CHRYSOTUS
blepharosceles Kow. 31, 33

CHRYSOTUS (*cont.*)
laesus (Wied.) 33
neglectus (Wied.) 31.
CINACHYRA
barbata 167
CINCHONA
early history 39
CINIFLO 18
CLADIUM
Mariscus 138
jamaicense 138
CLARK, W. E. LE GROS
on African fossil Primates 74
CLYPEOLELLA
Zizyphi * Hansf. 152
COELOCRABRO
ambiguus (Dahlb.) 14, 19, 31
leucostomoides Rich. 14, 30
COENOSIA
sp. 31
tricolor (Zett.) 31
COLMAN, J.
Polychaeta collected by 85
COMPOSITAE 41
CONIFERS
macroscopic photographs 51
CORDIA
heterophylla 131
nitidia 131
CORIOLIS FORCE 92
COUNCIL MEMBERS ELECTED 153
Fisher, J. M.
Kinnear, N. B.
Pearsall, W. H.
Philipson, W. R.
Sandwith, N. Y.
COUNCIL MEMBERS RETIRED 154
Bennet-Clark, T. A.
Cave, A. J. E.
Holden, H. S.
Pearson, A. A.
Sewell, R. B. Seymour
CRANE, H. H.
on Primula denticulata 74
CROSSOCERUS
anxius (Wesm.) 33
elongatulus (v. der Lind.) 14, 15, 19, 32, 33
CROTON
gossypifolium 150
sp. 121
CYNANCHUM
sp. 150
CYPERUS
flabelliformis 138

DARLINGTON, C. D.
Trail Award and Medal 154
DASYMASCHALON
clusiflorum 146
DAVALL, EDMUND
and Swiss Botany 179
DAY, J. H.
on Polychaeta 85
DEATHS REPORTED 155
Berridge, Miss E. M. 1
Bower, F. O. 73
Browne, Lady Isabel M. P. 1
Chatton, E. 1
DEATHS REPORTED (*cont.*)
Chaworth-Musters, J. L. 73
Dangeard, P. A.-C. 40
Dyer, B. S. 57
Grindley, Miss E. I. 73
Howard, Sir A. 2
Hurst, C. C. 40
Matthai, G. 1
Pugsley, H. W. 38
Wells, B. 40
DE BEER, G. R.
on Edmund Davall 179
DELF, E. M.
on Utilization of Seaweeds 1
DERRIS
sinuata 148
DEUTERAGENIA
hircana (F.) 18
DICHOTOMOUS KEY
and Adam Zaluziansky 40
DICOTYLEDONS
correlation and classification 40
DICRAEUS
vagans (Mg.) 33
DICTYLOMA
sp. 144
DIDYMOPANAX
sp. 127
DIKRANEURA
mollicula (Boh.) 32
DILEPTUS
gigas (film) 38
DILLENIACEAE 46
DIPSACACEAE 46
DISTICTIS
lactiflora 133
DOMINGOELLA
Deightoni * Hansf. 118
DONATIONS 197
Pilgrim Trust 56
Thomas Lawson MS. 3
DRAGESCO, M. JEAN
Films on :—
Deleptus gigas 38
Infusorian world 37
DROSERA
anglica 38
intermedia 39
rotundifolia 39
DROSOPHILA
melanogaster 77
simulans 77

ELASMOSAURUS 81
ELASMOTHERIUM 80
ELIZABETH, H.R.H. PRINCESS
Engagement—Address 2
signed Roll and Charter Book 73
EMPIS
aestiva Loew 33, 35
albinervis Mg. 33, 35
sp. 19, 31
ENTADA
africana 124
gigantis 124
EPISYRON
rufipes (L.) 14, 18, 22
EQUUS 78

ERITHALIS
parviflora 130
EUMENES 17
EUMENIDAE 12
EUPATORIUM
odoration 130
Oerstedianum 130
portoricensis 131
EUPHORBIACEAE 46
EUPTERYX
auratus (L.) 32
urticae (F.) 19, 32
vittatus (L.) 19, 32
EVOLUTION
mechanism of 75
EXHIBITION MEETING 48
Exhibitors :—
Adlard, J. E.
Bell, P. R.
Brooke, W. M. A.
Carpenter, G. D. Hale
Child, H.
Delf, E. M.
Fogg, G. E.
Garside, H. D.
Jane, F. W.
Jay, B. A.
Martin, M. T.
Moss, B.
Naylor, M.
Omarkhan, M.
Pearsall, W. H.
Price, W. R.
Puri, G. S.
Ross-Craig, S.
Royal Microscopical Society
Royal Society
Savage, S.
Stephenson, N. G.
Snelling, L.

FAGACEAE 47
FAGARA
martinicensis 127
FANNIA
similis (Stein) 31
sociella (Zett.) 31
spp.. 31
FARREA
sollasii 164
FASCIOLA
hepatica 76
FELL, H. B.
Trail Award and Medal 155
FELLOWS ELECTED
Abbis, H. W. 74
Abdin, G. 74
Amoroso, E. C. 74
Armitage, A. E. 74
Balfour, A. P. 74
Banerjee, S. 74
Bayne, Miss K. M. 74
Benthall, A. P. 74
Best, G. A. 74
Bevan, R. 74
Blake, A. E. 74
Blakelock, R. A. 74
Bowes-Lyon, Hon. D. 75

FELLOWS ELECTED (*cont.*)
Burrows, Miss E. 74
Burton, M. 74
Calder, Miss M. G. 74
Chaplin, Hon. A. F. C. H. 75
Das, M. C. 75
de Worms, C. G. M. 75
Duddington, C. L. 75
Durocher Yvon, F. 75
Ellis, E. A. 153
Fell, Miss H. B. 75
Fell, W. A. 75
Fisk, A. 75
Flynn, T. T. 75
Ford, E. B. 75
Ford, P. 75
Franklin, K. J. 75
Fraser, W. S. 75
Fryer, F. C. 75
Goodday, A. L. 75
Gregor, Rev. A. G. 75
Gregory, P. H. 75
Greig-Smith, P. 75
Harding, J. P. 75
Harrison, R. J. 75
Hayes, S. F. 75
Hellyer, A, G. L. 75
Hobby, B. M. 75
Hughes, Mrs. A. M. 75
Jayawardena, C. N. C. 75
Jones, J. W. 75
Khan, A. S. 75
Langham, H. G. 75
Lester, J. W. 75
Lewis, Miss P. 75
Lockie, G. D. 75
Manning, S. A. 153
Marples, B. J. 75
Marshall, H. S. A. 75
Matthews, H. I. 75
Munshi, D. M. 75
Nash-Wortham, J. R. H. 75
Nelmes, E. 75
Newth, D. R. 75
Newton, R. G. 75
Onabamiro, S. D. 75
Perkins, B. L. 75
Peterken, J. H. G. 75
Pichi-Sermolli, R. E. G. 75
Platt, J. W. O. 75
Prestwich, A. A. 75
Pryce-Jones, J. 75
Qureshi, Q. H. 75
Rhind, D. 75
Roychaudhury, S. P. 75
Russell, J. P. C. 75
Sherriff, G. 75
Simonian, V. H. 75
Snow, Mrs. C. M. 75
Sosa, J. M. 75
Stansfield, H. 75
Stephenson, Miss E. M. 75
Stephenson, N. G. 75
Sumner, W. L. 75
Talman, I. M. C. 75
Thornton, H. G. 75
Townley, Helen M. 75
Vanneck, Hon. A. N. A. 75
Webb, D. A. 75

FELLOWS ELECTED (*cont.*)
Webster, J. 75
Whitaker, Miss M. B. 75
White, D. J. B. 75
Williams, J. E. M. 75
Woodcock, G. S. 75
Worden, A. N. 153
Wright, A. S. 75
Wynne-Edwards, V. C. 153
FELLOWS REMOVED 155
FELLOWS WIHTDRAWN 155
FELLOWSHIP
numbers 157
FILMS
Boas and Pythons 163
Dileptus gigas 38
Funaria 38
Honey bee 38
Infusorian world 37
Outer Hebrides 57
South African Clawed Toad 163
FLACOURTIACEAE 46
FOREIGN MEMBERS ELECTED
Fage, L 75
Weberbauer, A. 75
FORSTERONIA
corymbosa 129
FUCOMYIA
frigida (F.) 18
FUCUS
spiralis 53
vesiculosus 52
FUNARIA
(film) 38
FUND
Library Restoration 158, 197
FUNGI
drawings 56
New Tropical 85, 116

GARCINIA
kydia 120
G.-B. INSTRUCTIONAL FILMS 38
GENTIANACEAE 46
GEODIA
barretti 2, 163
eoaster 166
parva 169
GESNERIACEAE 46
GMELINA
sp. 145
GORYTES
mystaceus (L.) 18
GRANTIA
compressa 166
GUAREA
sp. 148
GUATTERIA
dolichopoda 141
GYMNARCHUS 53
morphology of head 85

HALICHONDRIA
bowerbanki 166
HALICLONA
sp. 166, 167
HALICTUS
albipes (F.) 29
calceatus (Scop.) 29
fulvicornis (Kby.) 29
HALICTUS (*cont.*)
laevigatus (Kby.) 28
leucopus (Kby.) 29
leucozonius (Schr.) 29
malachurus (Kby.) 29
notatus (Kby.) 29
pauperatus Br. 29
rubicundus (Chr.) 29
tumulorum L. 29
zonulus Sm. 29
HANSFORD, C. G.
New Tropical Fungi III 85, 116
HARPACTUS
tumidus (Pz.) 14, 15, 27
HEBRIDES, OUTER
Survey (film) 57
HEDERA
helix 66
nepalensis 66
HELINA
duplicata (Mg.) 19, 27, 30
HIERACIUM
Prodromus of British spp. 38
HILARA
galactoptera Strobl. 31
HINE, R. L.
donation of Lawson MS. 3
HIPPARION 80
HIPPOCRATEA
sp. 118
velutina 117
HIRUNDO
rustica L. 101, 104
HOMING OF BIRDS
Discussion 85
Polish investigations 99
HONEY BEE
(film) 38
HOOKER LECTURE
Mechanism of Evolution (D. M. S. Watson) 75, 156
HYDROTAEA
irritans (Fall.) 31
sp. 27
HYMANIACIDON
perlevis 166
HYMENAEA
sp. 124
HYPERA 36
HYRACOTHERIUM 78

ILEX
montana 126
sp. 143
INDIA
Flora of British 66
INFUSORIAN WORLD
(film) 37
INOCARPUS
sp. 125
IRENE
sororcula Stev. 130
IRENINA
Aegiphilae * Hansf. 134
anastomosans Stev. 135
Barbacenniae * Hansf. 136
callista * Hansf. 134
cyclopoda Stev. 131
fidelis Toro 128
glabroides Stev. 132
hymenaeicola Stev. 124

IRENINA (*cont.*)
Lagerheimii Stev. 126
Linocieriae * Hansf. 128
longipoda Stev. 131
malloticola Yamamoto 121
Pileae * Hansf. 125
Pipturi * Hansf. 125
Premnae * Hansf. and Deight.
Schlegeliae * Hansf. 132
solanicola Stev. 131
Symphoniae * Hansf. 120
troloba Stev. 126
vilis Stev. 134
IRENOPSIS
curvata Stev. 118
Malpighiae * Hansf. 121
toruloidea Stev. 123

JARAMILLO-ARANGO, J.
on Cinchona 39
JASSIDAE 31

KODACHROMES
projector for showing 40

LABIATAE 46
LANNEA
Afzelii 118
LARUS
argentatus 91
LAWSON, THOMAS
MS. notebook 2, 3
LAWSONIA
alba 145
LEGESTRIA
senoculata 18
LEIOPELMA 56
LEMBOSIA
fallaciosa * Hansf. 152
Lophopetali * Hansf. 152
LEUCAGE 18
LEUCOSOLENIA
spp. 165
LIBRARY
Additions and Donations 194
Report, 155
LIBRARY RESTORATION
Donation 56
Fund 56, 158, 197
LICANIA
sp. 140
LIMNAEA
truncatula 76
LINDENIUS
albilabris (F.) 13, 15, 18, 19, 34
panzeri (v. der Lind.) 34
LINNAEAN COLLECTIONS
Report 156
LINNAEUS
Cast of Medallion 55
LINNEAN MEDAL
Dr. A. Arber 47, 154
LINOCIERIA
Cumingiana 129
LIRIOMYZA
sp. 33
LITSEA
sp. 146
LONCHOCARPUS
sp. 124

LOPHOPETALUM
toxicum 152
LUCILIA
caesar (L.) 27
sericata (Mg.) 27
sp. 19
LULWORTH AND EAST HOLME
Services training area 48, 156
LYGUS
pabulinus (L.) 35

MAGNOLIA
portoricensis 119
MAGNOLIACEAE 46
MAGNOLIALES 46
MALLOTUS
sp. 121
MALPIGHIA
glabra 121
MANIHOT
sp. 122
MARISCUS
jamaicensis 137, 138
MARTYNIACEAE 46
MAYNEORD, W. V.
nuclear physics in Biology 48
MEDALS
Linnean Gold 154
Trail 154
MEETINGS
alteration in dates 57
MEGALOCEROEA
linearis (Fuess.) 19
MELANAGROMYZA
aeneiventris (Fall.) 33
MELANOSTOMA
mellinum (L.) 27
MELINDA
caerulea Mg. 27
MELINIA
pullula (Zett.) 30
MELIOLA
aethiops Sacc. 124
Anacardii Zimm.
var. minor * Hansf. 127
apiculata * Hansf. 137
argentina Speg. 137
Arundinis Pat.
var. angulosa * Hansf. 138
bidentata Cooke 133
bignoniacearum Stev. 133
var. Tabebuiae * Hansf. 133
brevidentata Syd. 121
Callicarpae Syd. 135
circinans Earle 136, 137
cylindrophora Rehm 124, 135
Cyperi Pat. 137
didymopanicis P. Henn. 127
Distictidis * Hansf. 132
Entadae * Hansf. 124
Erithalidis * Hansf. 130
Fagarae-martinicensis * Hansf. 126
Forsteroniae * Hansf. 129
franciscana * Hansf. 123
Garciniae Yates
var. mangostana * Hansf. 120
ilicicola * Hansf. 126
inermis K. and C. 131

MELIOLA (*cont.*)
Inocarpi Stev. 125
janeirensis * Hansf. 121
juruana P. Henn. 124
linocieriicola * Hansf. 129
Magnoliae Stev. 119
mangostana Sacc. 119
manihoticola P. Henn. 121
Martiniana Gaill. 119
micromera Syd. 135
microspora Pat. and Gaill. 135
Mouririae Ciferri 119
Phoebes * Hansf. 136
polyodonta Syd. 122
Polysciatis Hansf. 127
Premnae * Hansf. 135
Psychotriae Earle 130
rizalensis Syd. 135
sauropicola Yates 122
Solani Stev. 131
sp. 130
Sydowi * Hansf. 122
Ulei * Hansf. 132
Vaccinii Stev. 128
Zizyphi * Hansf. and Thiruml. 126
MELITTOBIA
acasta (Walk.) 24
MELLINUS
arvensis (L.) 14, 18, 19
MEMECYLUS
subfurfuraceus 149
MEROMYZA Mg. 35
saltatrix (L.) 35
variegata Mg. 35
META
reticulata (L.) 25
METACRABRO
quadricinctus (F.) 32
METHOCA
ichneumonides Latr. 18
MICRATHENA
bifurcata Hahn 18
MICRO-SLIDE
history 54
MICROCHRYSA
flavicornis (Mg.) 31
polita (L.) 31
MIGRATION OF BIRDS 85
MITTERIELLA
zizyphina Syd. 153
MORENOELLA
Memecyli Syd. 149
MORUS
bassanus 91
MOUNTAIN HABITATS
photographs 54
MUSCA
corvina F. 18
MUSCID 31
MYDAEA
ancilla (Mg.) 31

NANNIPPUS 79
NATURE RESERVES
preservation 156
NAVIGATION
Bird 85
NEOLITSEA
sp. 151
NEOTENY
in a Newt 57
NOTOPTERUS 53
NUCLEAR PHYSICS
in Biology 48
NYMPHAEACEAE 46

OBITUARIES
Baker, F. H. 68
Berridge, E. M. 68
Chaworth-Musters, J. L. 193
Dangeard. P. A. C. 70
Dyer, B. S. 71
Grindley, E. I. 72
Pethybridge, G. H. 186
Pugsley, H. W. 187
Wells, B. 72
OCEANODROMA
leucorrhoa 91
ODYNERUS
laevipes Shuck. 16, 17, 36
spinipes (L.) 14, 17, 36
OEDALEA
holmgreni Zett. 31
OFFICERS ELECTED 154
President
de Beer, G. R.
Treasurer
Stern, F. C.
Secretaries
Barnes, B.
Hopwood, A. Tindell
OMARKHAN, M.
on Gymnarchus 85
ONCODES
gibbosus (L.) 30
ONESIA
sp. 27
ORIENTATION OF BIRDS
Methods 85
Physical Principles 94
Polish Investigations 99
ORTHOTYLUS
sp. 35
OSBORN, M. and E.
plant paintings 49
OSCINELLA
frit (L.) 33
OXYBELUS
uniglumis (L.) 14, 15, 29, 34

PAINTINGS
on vellum 54
plant 49
PARANOTHYREUS
cingulatis Pack. 34
PASSALOECUS
corniger Shuck. 36
PASSIFLORA
foetida 151
quadrangularis 151
PERIPLOCA
nigrescens 150
PEDAHACEAE 46
PHILAENUS
spumarius (L.) 18, 27
PHILOPHYLLA
heraclei (L.) 31

PHOEBE
costaricana 136
PHRAGMITES
sp. 139
PHRYMACEAE 46
PHYLLOMYZA
sp. 31
PHYSALIS
peruviana 131
PHYTOMYZA
ranunculi
var. albipes Mg. 31
sp. 33
PIERIS
rapae 39
PILEA
Parietaria 126
PILGRIM TRUST
donation 56
PIPTURUS
arborescentis 125
PIPUNCULUS
flavipes (Mg.) 31
PITHANUS
maerkeli (H. S.) 35
PLAGIOGNATHUS
arbustorum (F.) 19, 35
chrysanthemi (Wolff.) 35
PLANARIANS
land 85
PLEIOSAURUS 82
PLENOTOMA
diversifolia 133
POLEMONIACEAE 46
POLIETES
lardaria (F.) 18
POLISH INVESTIGATIONS
on homing of birds 99
POLLENIA
rudis (F.) 19, 27, 31
vespillo (F.) 18
POLYCHAETA
collected at St. Helena 85
POLYMASTIA
invaginata 167
magna 165
mammillaris (Müller) 165
POLYMORPHISM 50
POLYSCIAS
fulva 127
POMPILIDAE 12
POMPILUS
cinctellus 18
plumbeus (F.) 13, 14, 18, 20, 21, 22
trivialis Dahlb. 16, 17, 22
PREMNA
Cumingiana 135
nauseosa 135
odorata 134
PRESIDENT
Review 156
PRIMATES
African fossil 74
PRIMULA
denticulata 74
PRIOCNEMIS
perturbator (Harris) 22
PRUDHOE, S.
on Land Planarians 85
PRUDHOE, S. (*cont.*)
on Round and Flatworms 85
PSEUDELEPHANTOPUS
spicatus 131
PSYCHOTRIA
sp. 130
PUFFINUS
p. puffinus 91

RAMSBOTTOM, J.
on Adam Zaluziansky 40
new projector to show Kodachromes 40
RANDIA
sp. 142
RANUNCULUS
Flammula L. 74
RAVEN, C. E.
on Thomas Lawson 2, 3
REPORTS AND REVIEWS
President's 156
Treasurer's 157
Assistant Secretary's 155
REPRODUCTION
in sponges 163
RHAMPHOMYIA
tarsata Mg. 31
RHOPALUM
clavipes (L.) 35
RHYNCHOSPORA
corymbosa 137
RICINUS
communis 117
ROSE, F.
on Butterflies and Drosera anglica 38

SALICACEAE 46
SARCOPHAGA
nigriventris Mg. 30
sp. 18
SAUROPUS
sp. 122
SAVAGE, S.
Hon. Member Swedish Linnean Society 157
SCATOPHAGA
stercoraria (L.) 19, 27
SCHIFFNERULA
Cassiae * Hansf. 151
costaricensis * Hansf. 144, 150
Crotonis * Hansf. 149
Doidgeae Hansf. 150
Hippocrateae * Hansf. 116
mirabilis Hoehnel 151
Periplocae * Hansf. 150
Ricini * Hansf. 117
Scopariae * Hansf. 117
Solani * Hansf. 118
sp. 153
Spigeliae * Hansf. 117
SCHLEGELIA
sp. 132
SCHMIDELIA
sp. 147
SCIAPUS
platypterus (F.) 31
SCIARA
sp. 33
SCOPARIA
dulcis 117

SCYTOTHALIA
dorycarpa 53
SEAWEEDS
Commercial products 50
Utilization 1
SEGESTRIA
senoculata (F.) 18
SEPSIS
sp. 31
SEYNESIA
submegas P. Henn. 148
SIDEROXYLON
ferrugineum 146
sp. 128
SIPHNEUS 81
SMITH, M. A.
exhibit of living Newt 57
resignation as Zoological Secretary 157
SMITHIAN COLLECTION
Report 156
SOLANUM
acerifolium 144
callicarpaefolium 144
duplosinuatum 118
Englerianum 132
jamaicense 131
laurifolium 150
macrocarpon 118
Melongena 118
SOLENIUS
larvatus (Wesm.) 30
SPHECODES
crassus Thoms. 29
gibbus (L.) 29
SPHECOIDEA 12
SPIGELIA
Anthelmia 118
SPONGES
Geodia barretti 2, 163
reproduction in 163
SPORNE, K. R.
Correlation and classification in Dicotyledons 40
STACHYBOTRYELLA
bispora * Hansf. 149
STENOTUS
binotatus (F.) 19, 35
STIGMUS
solskyi Mor. 13, 14, 35
STURNUS
vulgaris L. 91
SUBERITES
carnosa 165
domuncula 165
SWEDISH AMBASSADOR
at Anniversary Meeting 153
SWISS BOTANY
and Edmund Davall 179
SYMPLOCOS
sp. 128, 145
SYMPHONIA
gabunensis 120
SYRPHUS
luniger Mg. 27
SYSTEMATICS ASSOCIATION
Annual Report 1946–47 i
joint meeting 58
SYTOTHALIA
dorycarpa 53
TABEBUIA
Berterii 133
TACHYDROMIA
claranda (Collin) 34
pallidiventris (Mg.) 31, 33
verralli (Coll.) 31, 34
sp. 31
TAMUS
communis Linn. 39
TARENTULA
accentuata (Latr.) 22
carinata Oliv. 22
TAXONOMIC RESEARCH
Discussion on organization 58
Speakers :—
Bor, N. L. 64
Burtt, B. L. 67
Crawford, G. I. 68
Evans, J. W. 61
Freeman, J. A. 58
Hopwood, A. T. 68
Kerrich, G. J. 67
Melville, R. 67
Metcalfe, C. R. 68
Milne-Redhead, E. 62
Osborn, T. G. B. 58
Smith, J. Wyatt 58
Thomas, A. S. 66
Trewavas, E. 59
Turrill, W. B. 66
TAXONOMY
lectures on 156, 185
TECOMA
pentaphylla 133
TETHYA
aurantium (Pallas) 165
TETRAPODS
Brain-case 40
THERIDION
notatum (L.) 25
redimitum (L.) 24, 25
tinctum Walck. 25
THORPE, W. H.
on Bird Orientation 85, 94
TIMBERS
photomicrographs 51
TITANOTHERIUM 78
TOAD
South African Clawed (film) 163
TRAIL AWARD AND MEDAL
Dr. C. D. Darlington 154
Dr. Honor B. Fell 154
TREASURER
Report and Account 157
TRIGONOTYLUS
ruficornis (Geoffr.) 19, 35
TRINACROMERIUM 81
TRITURUS
vulgaris 57
TROCHOSA
terricola (Thor.) 22
TROPICAL FUNGI 85, 116
TROPIDOSCINIS
gallarum Duda 33
TRYPOXYLON
albitarse F. 18
fabricator Sm. 18
figulus (L.) 14, 15, 23, 25
TURNERA
ulmifolia 149

Typhlocyba
sp. 32

Uggla, A. H.
at Anniversary Meeting 153

Vaccinium
reticulatum 128
Valerianaceae 46

Wareham
Local Enquiry 48, 156
Wasps
British hunting 3, 12
Watson, D. M. S.
on Mechanism of Evolution (Hooker Lecture) 75, 156
Wild Flowers (British)
drawings 56
Wilkinson, D. H.
on Bird orientation 85, 94
Wojtusiak, R. J.
on Polish investigations on Homing of birds 99
Worms
round and flat of West Indies and Surinam 85

Xenopus
laevis 163

Zaluziansky, Adam
dichotomous key 40
Zaphrentis 81
Zizyphus
sp. 126, 152
Zoological Secretary
resignation 157
Zostera 166

ERRATA.

Page 2, 8 lines from top— *for* indicates *read* indicated.

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CONTENTS

Page

Proceedings of the 160th Session 1

Communications printed in full or in abstract in the Proceedings 160 Session.

ADLARD, J. E. A collection of plant paintings by Mary and Emma Osborn 49

BARNES, B. White flowers in *Ranunculus Flammula* Linn 74

BELLAIRS, A. d'A., and R. WHEELER HAINES. The anterior brain-case of tetrapods, with a consideration of the interobital septum 40

BOR, N. L. On the Organization of Taxonomic Research 64

BRISTOWE, W. S. Notes on the habits and prey of twenty species of British hunting wasps 12

BROOKE, W. M. A. Drawings of Basutoland plants 49

BURKILL, I. H. The ontogeny of the stem of the Common Bryony, *Tamus communis* Linn. 39

BURTON, M. Non-sexual reproduction in sponges, with special reference to a collection of young *Geodia* 2, 163

CAMPBELL, J. W. Outer Hebridean Bird life.—The breeding of the Common Heron (*Ardea cinerea cinerea* L.), illustrating changes in status and habitat 57

CARPENTER, G. D. HALE. Polymorphism 50

CLARK, W. E. LE GROS. A review of the African fossil Primates discovered during the year 1947 74

DE BEER, G. R. Edmund Davall, F.L.S., an unwritten English chapter in the History of Swiss Botany.—Final Addendum 179

DELF, E. M. Commercial products derived from seaweeds 50

DELF, E. M. Utilization of Seaweeds 1

DISCUSSION on the Organization of Taxonomic Research 59

DISCUSSION on the orientation of birds on migratory and homing flights 85

EVANS, J. W. On the Organization of Taxonomic Research 61

FOGG, G. E. Water-colour drawings of blue-green Algae 51

GARSIDE, H. D. Water-colour drawing of Fungi 56

GRIGG, F. C. The history of the Micro-slide : Exhibited by The Royal Microscopical Society 54

HANSFORD, C. G. Tropical Fungi.—III. New species and revisions 116

HOOKER LECTURE.—The Mechanism of Evolution. By D. M. S. Watson 75

JANE, F. W. Photomicrographs of timbers 51

JARAMILLO-ARANGO, J. Established fundamental facts in the history of *Cinchona* 39

CONTENTS (*cont.*).

Page

JAY, B. A. Macroscopic photographs for the identification of Conifers 51

MARTIN, M. T. Some parasitic Red Algae 52

MAYNEORD, W. V. Some applications of nuclear physics in biology and medicine 48

MEDICI SOCIETY (THE). Recent water-colour drawings of British Wild flowers 56

MILNE-REDHEAD, E. On the Organization of Taxonomic Research 62

MOSS, B. Stages in development of the attaching discs of *Fucus vesiculosus* 52

NAYLOR, M. The liberation of the oospheres in *Fucus spiralis* and in the Australian fucoid *Scytothalia dorycarpa* 53

OBITUARIES 68, 186

OMARKHAN, M. The lateral sensory canals of larval *Notopterus* 53

PEARSALL, W. H. Photographs illustrating Mountain habitats 54

PRICE, W. R. A volume of paintings on vellum dated 1608 54

RAVEN, C. E. Thomas Lawson's Note-book 3

ROSE, F. Small white butterflies caught by *Drosera anglica* Huds 38

ROYAL SOCIETY, Manuscripts and drawings exhibited by the 54

SAVAGE, S. A book Herbarium made by Jacob Bobart the elder and his son (c. 1660–) . 55

SAVAGE, S. Cast of Medallion portrait of Linnaeus by Tobias Sergel, made by order of Queen Lovisa Ulrika for the museum at Drottningholm 55

SPORNE, K. R. Correlation and classification in Dicotyledons 40

STEPHENSON, N. G. Developmental adaptations of the primitive anuran genera, *Leiopelma* and *Ascaphus* 56

THORPE, W. H. Recent biological evidence for the methods of bird orientation. (Discussion on the orientation of birds) 85

TREWAVAS, E. On the Organization of Taxonomic Research 59

WATSON, D. M. S. *The Hooker Lecture.* The Mechanism of Evolution 75

WILKINSON, D. H. Some physical principles of bird orientation. (Discussion on the orientation of birds) 94

WOJTUSIAK, R. J. Polish investigations on homing in birds and their orientation in space. (Discussion on the orientation of birds) 99

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Catalogue of the Manuscripts in the Library of The Linnean Society of London.—Part 2. *Caroli Linnaei Determinationes in hortum siccum Joachimi Burseri. The text of the manuscript in the Linnaean Collections*, edited by Spencer Savage, F.L.S. London, 1937. (Pp. 78.) 13*s.* 4*d.* net.

—— Part 3. *Synopsis of the Annotations by Linnaeus and contemporaries in his Library of Printed Books.* By Spencer Savage, F.L.S. London, 1940. (Pp. 20.) 6*s.* 8*d.* net.

—— Part 4. *Calendar of the Ellis Manuscripts.* (*The Correspondence and Miscellaneous Papers of John Ellis, F.R.S.*) By Spencer Savage, F.L.S., Hon. Memb. Sv. Linné-sällsk. (Pp. vi, 104.) London, 1948. 25*s.* net.

'A Prodromus of the British *Hieracia*.' By the late H. W. Pugsley, B.A., F.L.S., has been published as Vol. 54 of the Society's Journal, Botany, comprising pp. iv, 356, and 17 plates. Copies are available for purchase by non-members, £3.